Mammalian Diversity on Mount Isarog, a Threatened Center of Endemism on Southern Luzon Island, Philippines

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Abstract

Field studies were conducted on Mount Isarog in southern Luzon Island between 1988 and 1995 in all native habitat types (lowland, montane, and mossy rain forest) from ca. 400 m to the peak at 1966 m elevation. Forty-three species of mammals are present: 2 insectivores, 25 bats, 1 primate, 11 rodents, 2 carnivores, and 2 ungulates. Five additional species, including three bats and two rodents, are known from nearby localities. During these studies, four species were recorded from Luzon for the first time: *Harpyionycteris whiteheadi, Harpiocephalus harpia, Kerivoula hardwickii,* and *Philetor brachypterus.* Three species are endemic to Mount Isarog (*Archboldomys luzonensis, Chrotomys gonzalesi,* and *Rhynchomys isarogensis*), one other is known only from southern Luzon (*Phloeomys cumingi*), and three others are widely distributed on but endemic to Luzon (*Otopteropus cartilagonodus, Apomys microdon,* and *Batomys granti*).

We suspect that more species of insectivorous bats and large fruit bats remain to be found on Mount Isarog, but our data indicate that insectivores, rodents, small fruit bats, and large mammals are probably completely sampled. Fruit bats are most diverse and abundant in the lowland rain forest, declining rapidly above the upper edges of lowland forest at ca. 1000 m elevation. Insectivorous bats also decline in diversity with increasing elevation, and with the exception of one species that was especially abundant at middle elevations (*Pipistrellus javanicus*), abundance followed the same pattern. Nonvolant small mammals increased markedly in diversity and abundance with increasing elevation, with most species absent below the lower edge of montane forest. All but one of the species of large mammals once occurred at virtually all elevations, but overhunting combined with deforestation has decimated populations at lower elevations.

Non-native mammals are virtually absent in natural habitat on Mount Isarog, even though several species are abundant in nearby agricultural and residential areas. Based on patterns observed on Mount Isarog and elsewhere in the Philippines, we propose the hypothesis that the richness of the native small-mammal community influences the success of non-native small mammal species in invading natural habitats: where few or no native species are present, non-natives flood into the forest, but where many native species are present, few or no non-native species are able to invade.

Bats that require caves as roosting sites are apparently among the most threatened species that occur on or near Mount Isarog; three such species (*Eonycteris robusta, Hipposideros bicolor,* and *H. pygmaeus*) may be locally extinct. Overhunting has greatly reduced the number of large flying foxes and all species of large mammals; in the current conditions of virtually no protection, at least one species (*Cervus mariannus*) may soon be extinct on the mountain. Several species that require old-growth lowland forest have been greatly reduced in number

by deforestation. Protection of the remaining forest, both old growth and second growth, is essential to the survival of a remarkable and unique set of species.

Introduction

At over 108,000 km^2, Luzon is one of the largest islands in the Pacific Ocean. With at least 21 endemic species of mammals (Heaney, 1993; Heaney et al., 1998; Rickart et al., 1998), it also supports one of the largest endemic faunas of mammals, especially when relative area is considered (Heaney, 1986; Heaney & Regalado, 1998; Heaney et al., 1998; Rickart & Heaney, 1991; Rickart et al., 1991). Indeed, it was the discovery of the exceptionally diverse rodent fauna of the mountains of north-central Luzon by John Whitehead in 1895 (Thomas, 1898) that led to much of the early interest in the mammals of the Philippines (Sanborn, 1952; Taylor, 1934). Repeated surveys of the highlands of northern Luzon have led to a common perception that the mammal fauna of Luzon may be the best known in the country (Manuel, 1935; Rabor, 1955; Sanborn, 1952).

However, recent studies have shown that this is unlikely to be the case. In particular, the discovery and naming of three highly distinctive endemic species of mammals from southern Luzon during the past 15 years (*Archboldomys luzonensis* Musser, 1982b; *Rhynchomys isarogensis* Musser & Freeman, 1981; *Chrotomys gonzalesi* Rickart & Heaney, 1991) and the earlier description of a small fruit bat that is widespread on Luzon (*Otopteropus cartilagonodus* Kock, 1969), plus the description of a new species of *Archboldomys* from northeastern Luzon (Rickart et al., 1998), clearly demonstrate the inadequacy of earlier faunal inventories. Moreover, until very recently, almost no information on the ecology and conservation status of mammals from Luzon was available (e.g., Oliver et al., 1993a; Ruedas et al., 1994).

In 1988, four of the present authors and several colleagues spent 4 months conducting surveys of mammals and other taxa in the southern Luzon region, beginning with Catanduanes Island and proceeding to Mount Isarog (Heaney et al., 1991; Fig. 1). We chose to focus on southern Luzon because preliminary data indicated that the Bicol Peninsula and associated smaller islands had a fauna somewhat distinct from that of northern Luzon, and it was clearly the more poorly known of the two regions (Heaney, 1986). Our work on Catanduanes resulted in a more complete understanding of the birds (Goodman & Gonzales, 1989) than was available previously (Gonzales, 1983), and in the first report on the mammals of that island (Heaney et al., 1991). Our initial studies on Mount Isarog, which immediately followed our fieldwork on Catanduanes, yielded an extensive assessment of the avifauna of the mountain (Goodman & Gonzales, 1990), an analysis of community structure of nonvolant small mammals along an elevational transect (Rickart et al., 1991), the description of the southern Luzon shrew-rat (*Chrotomys gonzalesi*) mentioned above, and one of the first surveys of tropical ants along an elevational gradient (Samson et al., 1997). In 1989, 1990, and 1993–1994, one of us (D. S. Balete) returned to the mountain for further faunal studies in conjunction with the development of a conservation management program for Mount Isarog National Park, which encompasses the entire mountain, and for research for a Master's degree thesis (Balete, 1995; Balete & Heaney, 1997).

In the course of this and other faunal inventories (Heaney et al., 1989; Rickart et al., 1993), it has become clear to us that knowledge of Asian mammals in general and Philippine mammals in particular is critically limited. Past studies, though yielding much important information, have rarely been conducted in an intensive, systematic fashion that yielded comprehensive faunal analyses of mammals for given regions. In particular, mammals that occur in low densities, those that occur at high elevations, and small species, especially insectivorous bats, have been inadequately sampled, so that our knowledge of local diversity patterns is quite poor. Moreover, as we have come to recognize that variation in diversity and abundance along elevational gradients plays a central role in determining general geographic patterns of diversity and abundance (Heaney et al., 1989; Rickart, 1993; Rickart et al., 1991), we have learned just how little precise information on diversity can be extracted from past surveys (Musser & Heaney, 1992). We have thus come to realize the great importance of establishing "benchmark sites," i.e., places where investigation is sufficiently intensive that we can develop an accurate picture of patterns of diversity, so that we may then evaluate the degree to which other studies may be incomplete indicators of diversity. We

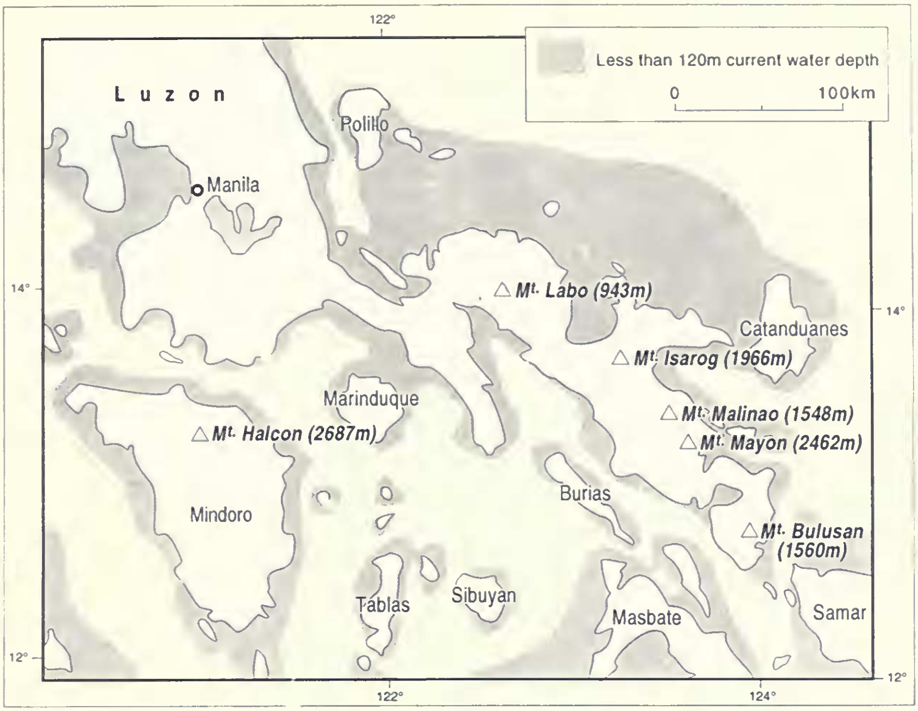

FIG. 1. Map of southern Luzon and adjacent regions, indicating the position of islands and mountains referred to in the text. The hypothesized extent of dry land during the late Pleistocene (ca. 18,000 years ago), when sea level dropped to 120 m below the present level, is shown.

chose Mount Isarog as one of the places where we would conduct such a benchmark study.

A final and more compelling reason drew us to choose southern Luzon as a study area. When Europeans first arrived in the Philippines, most of Luzon was covered by old-growth rain forest, which was the natural vegetative cover of nearly all of the island. By 1870, old-growth rain forest still covered over half of the land in the southern portion of Luzon and most of the adjacent smaller islands (Fig. 2). By the beginning of the American colonial period, in 1902, this had been reduced somewhat, but an acceleration in the rate of destruction of natural habitat was apparent. By 1960, rain forest cover was limited to high mountains and rugged, inaccessible regions, and by 1986 it had receded to cover at most 10% of the region (Fig. 2). An aerial survey in 1992 disclosed that forest on Mount Isarog was "slowly being degraded by numerous poaching operations" (Development Alternatives, Inc., 1992). Deforestation has increased the intensity of floods and droughts because little forest is present to soak up rainfall and release it gradually; monthly rainfall on Mount Isarog can exceed 2 m, as documented below. The function of forest as watershed protection is critical, and absence of watershed forests is now causing increasingly severe economic problems throughout the Philippines (Heaney & Regalado, 1998; Myers, 1988). Reduction and fragmentation of the native habitats will also make populations of animals increasingly vulnerable to extinction because small populations are more vulnerable than large populations to natural disasters (fires, floods, droughts, and disease) and to the direct effects of human disturbance (hunting and other forms of disruption). We viewed our study as an attempt to document the diversity of southern Luzon while an area still remains that supports most of the native mammal fauna. Our studies on the birds of Mount Isarog National Park, conducted concurrently with those on mammals reported here, have shown that 42% of the lowland birds once present on Mount Isarog are now locally extinct (Goodman & Gonzales, 1990). This finding clearly demonstrates that the native vertebrate species are highly vulnerable and raises the prospect that native mammal species may also have become locally extinct. This issue is addressed below.

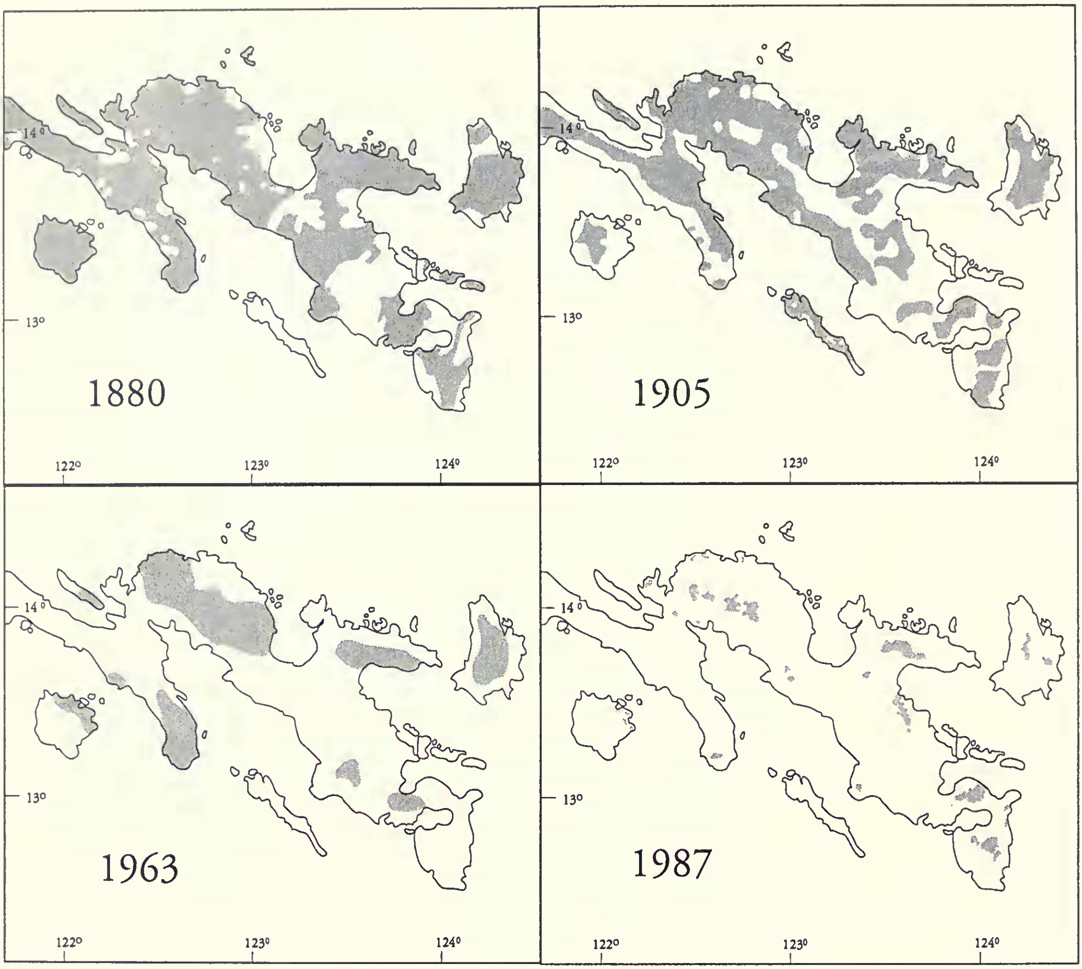

Fig. 2. Maps of forest cover on southern Luzon and adjacent islands in ca. 1870 (Anonymous, 1876), ca. 1900 (Anonymous, 1905), 1960 (Huke, 1963), and 1987 (National Mapping and Resource Information Authority, 1988), showing the progressive loss of old-growth forest on southern Luzon and adjacent islands. Most remaining old-growth forest fragments are restricted to areas above 1000 m elevation on isolated mountains or in rugged areas dominated by exposed limestone ridges.

This report summarizes distributional, systematic, and ecological information on all of the mammal species that we documented on Mount Isarog, and it presents the results of our elevational transect study of fruit bats, which parallels that of rodents and insectivores published elsewhere (Rickart et al., 1991). The purpose of this paper is to summarize all of the currently available information on the mammal fauna of the park. Because of the importance of, but lack of previous information about, mossy forest habitats and mammal communities, we provide more extensive and detailed data on this than on any other habitat.

Study Area and Methods

Geology of the Mount Isarog Area

Mount Isarog is an extinct volcano surrounded by lowland plains. Rising to 1966 m, it is the highest forested peak on southern Luzon; the only higher peak, Mount Mayon (2462 m), is an active volcano covered by barren volcanic ash over most of its upper elevations. Southern Luzon is a part of the Eastern Philippine Rim Structural Region and lies just to the west of the northern portion of the Philippine Trench, where the Pacific Plate is actively subducted below the Philippines (Hamilton, 1979; Holloway, 1981). The geological history of the area is complex (Hall, 1996).

Recent evidence indicates that the southeast portion of Luzon originated as the northernmost extension of an arc system that gave rise to modern Samar and much of Mindanao. This arc system originated to the southeast of its current location and came into close juxtaposition with central and northern Luzon (and the central and western Visayas) only in the late Miocene/early Pliocene (Fuller et al., 1983; Hall, 1996; Mitchell et al., 1986). The Philippine Fault, which runs along the eastern edge of the Bicol Peninsula to its northern tip, where it then trends northwestward and forms the boundary between southern and central Luzon, is associated with the ongoing interaction between these two major land masses (Hamilton, 1979).

Volcanic activity and uplifting during Pliocene to Recent times associated with this subduction has produced 12 stratovolcanoes in the Bicol arc of southern Luzon, with three especially prominent basaltic/andesitic cones (Fig. 1): Mount Isarog (1966 m), Mount Mayon (2462 m), and Mount Bulusan (1558 m), as well as islands such as Catanduanes, which lies about 60 km to the east of Mount Isarog (Hamilton, 1979; Hashimoto, 1981; Philippine Bureau of Mines, 1963). Dated volcanic materials from the region of Mount Malinao (Fig. 1) are young, the oldest dated at only 3.2 and 3.4 million years ago (Ma), with many dates in the range of 0.4–0.16 Ma, and some are current (Knittel-Weber & Knittel, 1990). To the best of our knowledge, the volcanics from Mount Isarog have not been dated. The region is subject to frequent earthquakes; we experienced one recorded at 6.9 on the Richter scale during our 1988 season on Catanduanes, and we felt frequent minor shocks on Mount Isarog during the following months.

During the late Pleistocene (i.e., from about 25,000 to about 10,000 years ago), sea level dropped to about 120 m lower than at present (Fairbanks, 1989; Heaney 1986, 1991), uniting many of the current Philippine islands into larger islands. The present island of Luzon is the largest but not the only land mass that made up the late Pleistocene island of Greater Luzon; other portions formed the current Catanduanes, Marinduque, and Polillo, as well as some smaller islands (Fig. 1).

Climate of Mount Isarog

Mount Isarog lies in one of the principal typhoon tracks in eastern Asia, and rainfall is thus both abundant and seasonal, with a period of maximum rainfall from June to December and a relatively dry period roughly from January through May. The mountain usually is subject to severe storms from September to December. Mean annual precipitation at Naga City (elevation ca. 50 m, ca. 20 km west of the summit, data for 37 years) is 235 cm, with minimum and maximum monthly means of 6.9 and 30.9 cm in March and November, respectively (Manalo, 1956). Weather conditions varied during the duration of our study. In March 1988, rain was frequent and often heavy, and soils generally were saturated. In late April and early May 1988, rain was infrequent, mean subcanopy air temperatures were warmer, and lower elevations were conspicuously drier. Even on rainless days, however, areas above 1500 m were subject to regular dense fog, resulting in significant surface condensation. During the 1988 study period, subcanopy air temperature ranges were 17.5–30°C at 475 m and 10.0–23.9°C at 1750 m elevation.

Limited data from the central Philippines indicate that mid-elevation mountain regions (800–1100 m) receive up to three times as much rainfall as adjacent lowlands (Heideman & Erickson, 1987); we therefore anticipated that annual rainfall high on the mountain would be 5,000 mm or more. Balete (1995) measured rainfall at 1650 m (Site 18) on 141 days from the last week of November 1993 to the middle of May 1994 and recorded 5,713 mm. He estimated that about 8,800 mm fell during the 6-month wet season (which began in September), based on comparison with the adjacent lowlands, and that about 12 m fell during the entire year. Figure 3 shows that the heaviest precipitation occurred during December (daily mean of 74 mm, range 0–144 mm) and the least in February (daily mean of 20 mm, range 0–97 mm). The adjacent lowlands near Naga City received 1,112 mm during the same days that 5,713 mm fell at the 1650 m site, with total precipitation from 1 November 1993 to 15 May 1994 of 1,422 mm. Monthly totals (and daily means) for the lowlands ranged from 34.6 mm (1.2 mm) in February to 883.2 mm (28.5 mm) in December.

The temperature range at 1550 m (Fig. 4) measured by Balete (1995) was similar to that recorded during 1988 (Rickart et al., 1991), with a low of 10.0°C in February 1994 to a high of 24.5°C

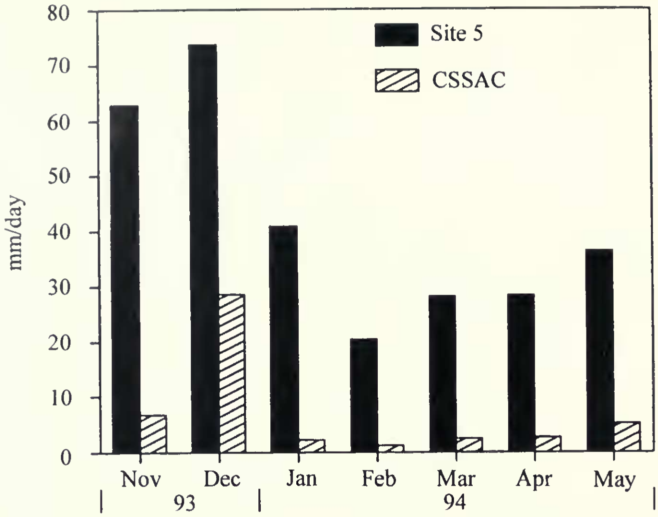

FIG. 3. Mean daily rainfall on Mount Isarog in mossy forest at 1550 m elevation (Site 5) and at 60 m elevation, Camarines Sur State Agricultural College, in the adjacent lowlands, November 1993 to May 1994. Number of days of observation at Site 5 (1550 m) were 7 (November), 27 (December), 31 (January), 28 (February), 28 (March), 8 (April), and 12 (May).

in March 1994. In comparison, the lowlands near the base of the mountain had much higher temperatures. Average monthly low temperatures from November 1993 to May 1994 ranged from 20.9°C in February to 22.1°C in November; the lowest temperature recorded, 17.0°C, was attained on 17 February. Average monthly highs during this period ranged from 34.8°C in May to 29.9°C in January; the highest temperature, 36.0°C, was reached twice, on 11 April and 3 May. In general, temperature showed little variation throughout the year (Fig. 4), with most seasonality instead being associated with rainfall.

Study Sites

Mount Isarog (summit at approximately 13°40′N, 123°23′E) has a form typical of many extinct volcanoes in the Philippines (Figs. 5 and 6). The top of the mountain consists of a semicircular ridge (1850–1950 m elevation) constituting the western flank of the former volcanic cone. The western and southern slopes are moderately steep and are cut by several large river channels. The eastern side, bordering the large interior crater, is extremely steep.

On the western and southern slopes of Mount Isarog, the natural vegetation below 900–1000 m was lowland dipterocarp forest (sensu Brown, 1919) characterized by a complex multistoried structure, heavy buttressing of canopy trees, high tree species diversity with a predominance of Dipterocarpaceae, abundant lianas, relatively few epiphytes, and an open understory with sparse ground cover. At the time of our studies, the surrounding lowland plains and the western and southern slopes of the mountain up to about 400 m were entirely deforested with the exception of a few small, isolated patches of secondary forest along steep river channels. Between 400 and 800 m, most areas of forest had been cut for timber production and cleared for agriculture. Remnant dipterocarp forest below 800 m was heavily disturbed and confined to river channels, but was generally contiguous with old-growth forest at higher elevations (in this publication, we refer to "old-growth" rather than "primary" forest in recognition of the disturbance associated with rattan and medicinal plant collectors and the potential for some small-scale clearing in the past). In the vicinity of the Panicuason Reforestation Station (Site 1; 475 m), many areas between 400 and 600 m that were contiguous with secondary forest had been replanted with a mixture of fast-growing trees, including exotic Amazonian mahogany (*Sweitenia macrophylla*) and an exotic legume locally called *ipil-ipil* (*Leucaena leucocephala*). By 1992, most of the grassland on the southern slope up to 500 m had been replanted with narra (*Pterocarpus indicus*), as well as the non-native trees

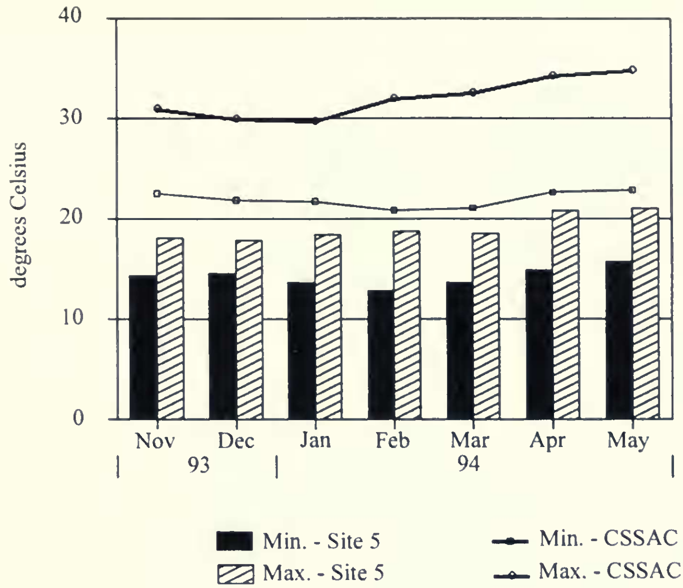

FIG. 4. Average minimum and maximum temperature on Mount Isarog at 1550 m elevation (Site 5) and at 60 m elevation in the adjacent lowlands (Camarines Sur State Agricultural College), November 1993 to May 1994 (see Climate section).

Falcata sp. and *Gmelina* sp., as part of a local community reforestation program.

During the 1988 study, the lower limit of old growth forest on the western and southern sides of the mountain was at about 900 m. Above this altitude, human disturbance was limited to occasional collection of rattan (*Calamus* and allied genera) and medicinal plants, and to hunting of birds and the few remaining monkeys (*Macaca fascicularis*), pigs (*Sus philippensis*), and deer (*Cervus mariannus*). Above 900 m on the western slope was a steep escarpment of about 100 m constituting a zone of transition between lowland dipterocarp forest and montane forest (midmountain forest, sensu Brown, 1919; lower montane rain forest, sensu Whitmore, 1984). Montane forest, which extended up to ca. 1500 m on the western and southern slopes, was characterized by an open, two-storied canopy structure, a transition from tree buttresses to stilt roots, a reduction in the number of dipterocarps with an attendant increase in oaks (*Lithocarpus*), a well-developed understory, abundant lianas and vascular epiphytes, and development of soils with high organic content. Above 1500 m, there was a gradual transition from montane forest to mossy cloud forest (upper montane rain forest, sensu Whitmore, 1984), which continued to the summit. Tree size and woody plant species diversity continued to decline and epiphyte loads increased (particularly mosses and liverworts). Additional photographs and descriptions of the study area were provided by Goodman and Gonzales (1990) and Heaney and Regalado (1998).

We conducted studies on Mount Isarog during three periods. During the first (1–30 March and 20 April–7 May 1988), we surveyed small mammals along an elevational transect on the western side of the mountain (Fig. 5, Sites 1–6), with two field teams operating simultaneously at different sites during most of the study. The transect consisted of six study sites centered at 475, 900, 1125, 1350, 1550, and 1750 m elevation (Fig. 5); studies at these sites formed the basis for publications on birds (Goodman & Gonzales, 1990), ants (Samson et al., 1997), and nonvolant small mammal distribution and ecology (Rickart et al., 1991). During the second period (November 1989–February 1990), we surveyed sites on the southern side of the mountain (Fig. 5, Sites 7–17); investigations were less extensive during this phase. During the third period (November 1993–May 1994), D. S. Balete returned to the western side of the mountain and conducted a capture–mark–recapture study at ca. 1650 m (Site 18), between Sites 5 and 6 (Balete, 1995). Brief site descriptions and inclusive dates of survey follow.

SITE 1—4 km N, 18 km E Naga, 475 m elev.,

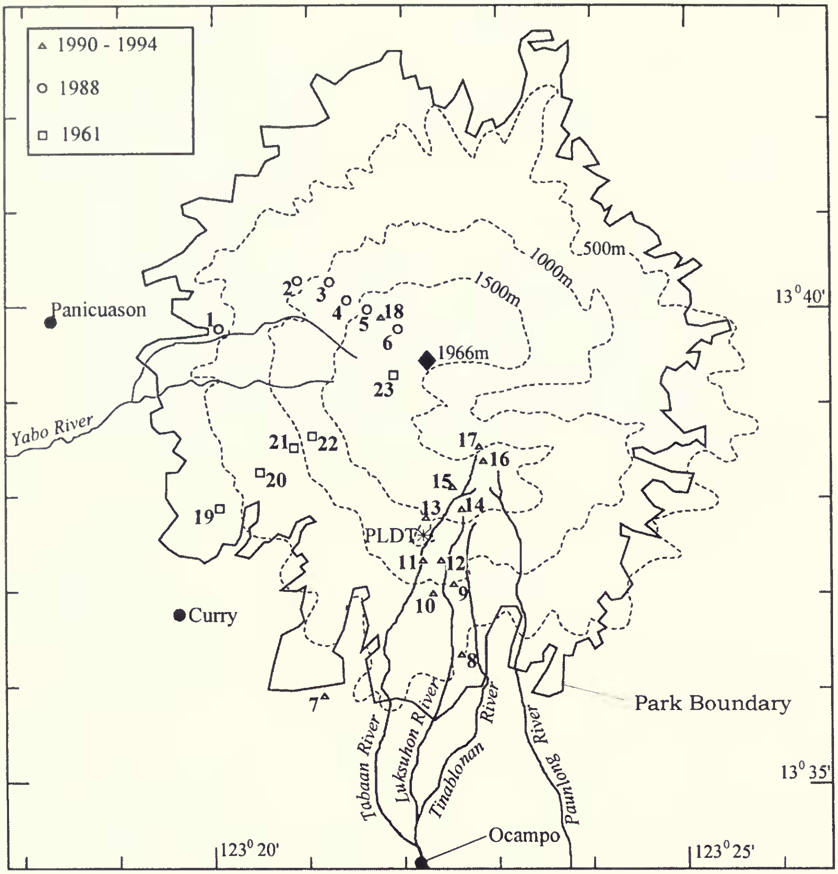

FIG. 5. Map of Mount Isarog showing the boundaries of the National Park and location of sites described in the text. Modified from Goodman and Gonzales (1990). Circles show the locations of 1988 sampling sites; triangles indicate the 1989–1994 sites; squares show the approximate locations of Rabor's 1961 sites "above Curry." "PLDT" marks the location of a Philippine Long Distance Telephone relay station.

13°40′N, 123°20′E (3–11 March; 4–8 May 1988). Sampling at this site was conducted in the vicinity of the Panicuason Reforestation Station in a mosaic of disturbed lowland dipterocarp forest adjacent to the Yabo River, a ca. 25-year-old forest plantation of a non-native legume (*Leucaena leucocephala*) and mahogany (*Vitex* sp.) with a well-developed understory of native vegetation and brushy or open habitat used for agriculture and grazing. Sampling was done in disturbed forest and forest plantation areas along the steep riverbanks. In both habitats there was an extensive understory of figs (*Ficus* spp.), piper (*Piper* spp.), saplings (primarily Dipterocarpaceae), small palms, and tree ferns (*Cyathea* spp.). Woody lianas were abundant in secondary forest, but most of the rattan had been harvested. There was a sparse ground cover of ferns and herbaceous dicots, with a thin layer of leaf litter over stony soil composed of weathered volcanic rock.

During the period of 23–31 March, several members of the crew, led by P. C. Gonzales, worked the area of scrubby second-growth forest, tree plantations, and agricultural land just below the Reforestation Station. They focused on surveys of birds (Goodman & Gonzales, 1990) but also captured bats and one *Crocidura grayi* and one *Phloeomys cumingi*. Because the bats were captured incidentally to other work, they are not included in our standardized comparison of sites.

SITE 2—5 km N, 20 km E Naga, 900 m elev., 13°40′N, 123°21′E (3–11 March, 30 April–4 May 1988). Located at the base of a steep escarpment (up to 45° slope) in an area of lowland dipterocarp forest with some elements of montane forest (Fig. 7), this site was a mosaic of old-growth forest,

FIG. 6. West face of Mount Isarog, from below Site 1 at ca. 300 m elevation, showing deforestation at lower elevations. May 1988, L. R. Heaney.

recently logged areas, and small areas of recent agricultural cultivation. Our efforts were concentrated in old-growth dipterocarp forest with a broken canopy at 20–30 m. The largest trees had diameters at breast height (dbh) of 0.5–1.5 m and moderate buttress development. The understory consisted of tree ferns, bamboo (*Bambusa* spp.), small palms, and saplings. Woody vines, climbing bamboo (*Schizostachyum* spp.), and climbing pandans (*Freycinetia* spp.) were common, and some rattan was present. Vascular epiphytes, including orchids, ferns, and pitcher plants (*Nepenthes* spp.), were common, and some moss was present on tree trunks and on dead wood. There was a moderate ground cover of pandans, ferns, and sedges (Cyperaceae). Leaf litter was not extensive, but there was a moderate humus layer.

SITE 3—4.5 km N, 20.5 km E Naga, 1125 m elev., 13°40′N, 123°22′E (23–30 March, 26 April–4 May 1988). The third site was located in lower montane forest (Fig. 8) with an overall slope of ca. 25°; canopy trees ranged from 18 to 25 m in height with dbh from 0.25 to over 0.5 m. Most large trees were not buttressed. Some moss was common on both dead wood and live trees. At both this and the 1350 m site, the understory consisted of saplings, tree ferns, and arborescent palms, with an extensive ground cover of pandans, sedges, and small ferns. Woody vines, climbing bamboo, and climbing pandans were common, as were strangler figs. Abundant epiphytes at both sites included pitcher plants, orchids, and ferns. Leaf litter was extensive, and there was a fairly thick and continuous layer of humus.

SITE 4—4 km N, 21 km E Naga, 1350 m elev., 13°40′N, 123°22′E (12–24 March, 25–30 April 1988). This site had an average slope of ca. 30° and was situated in upper montane forest with a low canopy of 12–20 m. Canopy trees had dbh ranging from 0.3 to more than 0.5 m, with little buttressing. Old logs had heavy moss cover, but moss was uncommon elsewhere on the forest floor. The trunks of all but the youngest trees had moderate moss cover. There was extensive leaf litter and a well-developed humus layer in most areas. Canopy trees had small (2–6 cm) leaves; oaks (*Lithocarpus* spp.) were common. Understory, vines, and epiphytes were similar to those at Site 3.

FIG. 7. Old-growth lowland forest habitat at Site 2, 900 m elevation. March 1988, E. A. Rickart.

FIG. 8. Old-growth montane forest habitat at Site 3, 1125 m elevation. March 1988, L. R. Heaney.

SITE 5—4 km N, 21.5 km E Naga, 1550 m elev., 13°40′N, 123°22′E (12–20 March, 19–26 April 1988). This site was in transitional montane–mossy forest in an area with an average slope of 30° and was bounded by steep ravines (Fig. 9). The canopy was at 10–15 m and was broken by many natural treefalls. Canopy trees had dbh of 15–40 cm with no buttressing but often with moderate stilt-root systems; leaves were small (2–6 cm). On steep terrain, lower trunks of trees were sharply inclined. The understory consisted of small shrubs, saplings, and tree ferns, with a ground cover of ferns, pandans, orchids, small dicots, and mosses. Climbing bamboo, rattan, and particularly climbing pandans were abundant. Vascular epiphytes were numerous, including orchids, ferns, and pitcher plants. Moss was very abundant, reaching depths of 10 cm in some areas but not covering all subcanopy surfaces. At both this and the 1750 m site, there was abundant leaf litter and a deep humus layer.

SITE 6—4 km N, 22 km E Naga, 1750 m elev., 13°40′N, 123°22′E (21–28 March, 20–25 April 1988). This site was situated in well-developed mossy forest (Fig. 10). The terrain was steep, ranging from 30° to 60°. The canopy was at 5–12 m and was broken by numerous treefalls. The largest trees had dbh ranging from 10 to 50 cm. Most trees had elaborate moss-covered stilt-root systems that often exceeded 2 m in basal diameter. Trees growing on the steepest slopes had nearly horizontal main trunks bearing vertical branches that formed the low canopy. Dominant trees included species of Lauraceae, with small lobate, serrate, or lanceolate leaves, and large, branching tree ferns. All surfaces below the canopy were covered with thick mats of mosses and liverworts.

The next phase of fieldwork was conducted on the southern side of Mount Isarog, barangay Del Rosario, Ocampo municipality, from November 1989 to February 1990 by a group led by D. S. Balete. This work was part of an effort to develop a management plan for Mount Isarog National Park.

SITE 7—Sitio Guinaban, ca. 100 m elev. (November 1989). We set up one 6-m net for one

FIG. 9. Old-growth transitional montane–mossy forest habitat at Site 5, 1550 m elevation. 24 April 1988, L. R. Heaney.

night in a banana (*Musa*) plantation for 2 hr and netted a single *Eonycteris spelaea*.

SITE 8—Sitio Dos; 4.7 km N, 0.2 km E Ocampo Munic., 300 m elev., 13°36′15″N, 123°23′30″E (19–22 November 1989). This site was an agricultural area with a narrow strip of remnant secondary forest along Luksuhon River. Mist nets and snap traps were set in remnant forest and along the edges of abaca and coffee plantations. Agricultural crops included maize, cassava, coffee, sweet potato, squash, and coconut. Cultivated trees included jack fruit (*Artocarpus heterophylla*), pili (*Canarium luzonicum*), star apple (*Chrysophyllum cainito*), mango (*Mangifera indica*), avocado (*Persea americana*), and guava (*Psidium guajava*). Forest trees taller than 20 m were rare and consisted mainly of tangid (*Cananga odorata*), rarang (*Erythrina subumbrans*), lumboy (*Syzygium* spp.), and figs (*Ficus* spp.).

SITE 9—Sitio Dos, 5.8 km N, 0.1 km E Ocampo Munic., 500 m elev., 13°36′48″N, 123°23′30″E (22–25 November 1989). This site was a remnant patch of secondary lowland forest on a rocky slope along Luksuhon River. The patch of forest was bounded by grassland with introduced grasses (*Imperata cylindrica, Sorghum nitidum,* and *S. halepense*). Netting and trapping sites included a patch of abaca (*Musa textilis*).

SITE 10—Sitio Anangi, 5.6 km N, 0.6 km W Ocampo Munic., 475 m elev., 13°36′43″N, 123°23′30″E (18–19 December 1989). The site was within an abaca plantation with very little remaining forest. Here we encountered a dark and spacious cave within a formation of huge rocks on the side of a sloping hill. Trees selectively retained to provide shade to abaca consisted mostly of *Erythrina subumbrans.*

SITE 11—Luktob, 6 km N, 0.9 km W Ocampo Munic., 475 m elev., 13°36′56″N, 123°23′30″E (18–19 December 1989). This site, along the steep bank of Tabuan River, centered on five shallow tunnels that, according to local residents, were dug by retreating Japanese soldiers near the end of World War II. Some tunnels were U-shaped, with both ends opening toward the river, whereas others were dug straight into the steep bank. A narrow strip of lightly disturbed forest surrounded the site. Signs of recent log extraction were evident. Most land above this forested strip was in use for agriculture.

SITE 12—Pasto, 6.1 km N, 0.3 km W Ocampo Munic., 700 m elev., 13°37′N, 123°23′30″E (27–29 November 1989). This site included disturbed forest, second-growth vegetation, and cleared pasture and agricultural land. Pure stands of mountain agoho (*Gymnostoma rumphianum*) occurred in areas close to Luksuhon River and Tabuan River. Figs, tree ferns, and rattan were abundant in the forested portion. Disturbed forest with trees up to ca. 20 m in height occurred along the Tabuan River. We found several large flowers of *Rafflesia* at this site. Upturned soil on the forest floor indicated that wild pigs were common in this area. A portion of this site, along Luksuhon Creek, said to have been settled originally by the Agta (an ethnically distinct group that traditionally engaged in hunting and gathering), remained cleared and was planted with maize, upland rice, and sweet potato. Adjacent to this clearing was a pastureland covered with grass and low stands of guavas. During our survey, half a dozen cattle and several water buffalos were seen grazing here.

SITE 13—Pasto, 7 km N, 0.1 km W Ocampo Munic., 900 m elev., 13°37′26″N, 123°23′30″E (7–9 December 1989). This site was in a strip of disturbed lowland dipterocarp forest on a ridge

FIG. 10. Old-growth mossy forest habitat just below the summit of Mount Isarog at ca. 1900 m elevation. March 1988, E. A. Rickart.

along the Tabuan River. Mountain agoho was common, especially along trails. Forest canopy was ca. 20 m high. The site was marked with many foot trails used by local people, who regularly gather rattan; in 1989–1990, the rattan had been badly depleted. We observed several mature almaciga (*Agathis damara*) on this site, mostly near the steep bank of the Tabuan River.

SITE 14—7.5 km N, Ocampo Munic., 1100 m elev., 13°37′43″N, 123°23′30″E (10–13 January 1990). This site was in predominantly old-growth forest, with some signs of recent logging, on a ridgetop overlooking the source of the Luksuhon River. The forest, with a canopy height of ca. 25 m, was transitional between lowland and montane types. Few trees had large buttresses. Palms and tree ferns were abundant, and figs also were present. Rattans, mostly immature because of overharvesting, were common. Climbing bamboos and pandans were abundant. Several trails cutting through this site were extensions of the ones from Site 12 and remained actively used by rattan gatherers and occasional tree cutters.

SITE 15—7.9 km N, 0.1 km E Ocampo Munic., 1300 m elev., 13°37′59″N, 123°23′30″E (7–10 January 1990). This site was in old-growth montane forest close to the Tabuan River. The forest canopy height was ca. 25 m, and most of the trees were without buttress roots. Climbing pandans were common. Tree ferns, ground ferns, and palms were abundant. Rattans were common, but there were signs of recent harvesting. Thick moss matted the base of tree trunks and soggy ground. Ephiphytes, including orchids, ferns, and pitcher plants, were abundant.

SITE 16—8.6 km N, 0.6 km E Ocampo Munic., 1500 m elev., 13°38′21″N, 123°23′30″E (7–10 January 1990). This site was in old-growth upper montane forest in a narrow valley. Canopy trees were mostly without buttresses, but stilt roots were not uncommon. The canopy was broken and the forest floor was abundantly covered with leaf litter, mosses, ferns, ground orchids, and herbaceous plants. Tree ferns, rattans, and climbing pandans were very common. Climbing bamboos were uncommon. Tree trunks and branches usually supported an abundant cover of mosses as well as orchids and ferns. Casts of earthworms were common on the forest floor.

SITE 17—8.9 km N, 0.8 km E Ocampo Munic., 1700–1800 m elev., 13°38′32″N, 123°23′30″E (31 December 1989–4 January 1990). This site was in mossy forest close to the highest peak on the east side of Mount Isarog. Canopy trees were short, ca. 15 m, and the canopy itself was highly broken. The forest floor was constantly wet and covered with thick leaf litter and matted mosses. Trees with stilt roots were common; those with buttresses were rare. The forest floor vegetation consisted mainly of herbaceous plants, ground orchids, and ferns. Trees were usually abundantly covered with mosses from trunk to canopy. Climbing pandans were common. Epiphytes consisting of dwarf orchids and ferns were abundant. Casts of earthworms were common on the forest floor.

SITE 18—4 km N, 21 km E Naga, 1650 m elev., 13°40′N, 123°22′E (November 1993–May 1994). This was the site for the mark-and-recapture study of small mammals conducted in 1993–1994 by D. S. Balete (Balete, 1995; Balete & Heaney, 1997). Data reported here include summaries of data from Balete and Heaney (1997) as well as more detailed information not published elsewhere. This site lies between Sites 5 and 6 and was generally similar to Site 5 in canopy height and forest structure. Thirty-six tree species, representing 23 families, with a total density of ca. 26 trees/100 m^2, were recorded within a 1 ha area at this site (Table 1). The canopy was 9–12 m in height, and the trees were thickly covered with mosses and epiphytic orchids and ferns (*Huperzia*, *Selaginella*, *Hymenophyllum*, and *Trichomanes* spp). Climbing pandans were attached to many of the trees. The dominant tree species included *Eugenia* (= *Syzygium*) spp. (Myrtaceae), *Tricalysia fasciculata* (Rubiaceae), and *Elaeocarpus argentes* (Elaeocarpaceae). Tree ferns (*Cyathea* sp.) were also a dominant group. Forest floor vegetation included many ground ferns (e.g., *Dipteris conjugata*) and herbaceous plants (e.g., *Languas scabra* and *Sarcandra glabra*). Rattans were also an abundant component of understory vegetation.

The density of invertebrates at this site was documented by Balete (1995) from December 1993 to April 1994. Amphipods were the most abundant group, with a mean density of 137 individuals/m^2 (range 78–238 individuals), followed by diplopods with 53 individuals/m^2 (range 30–88 individuals; Table 2). Biomass (Table 3), however, was highest for earthworms at 3.28 g/m^2 (range 1.02–6.40 g), followed by amphipods at 1.25 g/m^2 (range 1.06–1.66 g).

We also have included Rabor's 1961 collection of mammals from the southwest side of Mount Isarog (Baranggay Curry, Pili Municipality; Rabor, 1966). This collection, deposited at several museums in the United States, included the holotypes of two taxa of murid rodents endemic to Mount Isarog: *Archboldomys luzonensis* and *Rhynchomys isarogensis* (Musser, 1982b; Musser & Freeman, 1981). However, we have not been able to locate any field catalog or notes pertaining to Rabor's collection other than his subsequent short account of the expedition (Rabor, 1966). Elevational data were taken from the labels of

TABLE 1. Summary of vegetation analysis in the mossy forest on Mt. Isarog, showing the basal area and density (trees/100 m^2) of each species sampled.

Species	Total basal area (cm^2)	Trees/ 100 m^2
Syzygium spp.	28,726.9	4.1
Tricalysia fasciculata	626.6	2.9
Cyathea spp.	918.6	2.6
Elaeocarpus argentes	10,766.9	0.7
Rapanea arvenis	2,208.3	1.6
Weinmannia luzoniensis	5,276.6	0.9
Symplocos modesta	609.3	1.2
Ilex halemenses	4,647.1	0.5
Adinandra elliptica	3,921.8	0.5
Eurya nitida	2,008.6	1.0
Helicia cuningiana	272.6	1.1
Daphnipyllum luzonense	675.4	1.0
Glochidion rubrum	1,862.2	0.5
Claoxylon brachyandrum	711.9	0.7
Psychotria lucida	132.6	0.6
Persea philippinensis	519.0	0.5
Clethra lancifolia	232.1	0.5
Vaccinium spp.	791.1	0.4
Lithocarpus budii	172.1	0.5
Symplocos conchinchinensis	236.6	0.4
Geniostoma rupestre	56.7	0.4
Plachonella linggensis	434.0	0.3
Symplocos sp.	261.2	0.3
Symplocos cumingiana	799.6	0.2
Macaranga dipterocaprifolia	651.1	0.2
Schima sp.	488.4	0.2
Ilex crenata	136.9	0.2
Melastoma sp.	15.7	0.2
Litsea perottittii	490.4	0.1
Cryptocarya elliptifolia	113.1	0.1
Veronia arborea	132.7	0.1
Ficus septica	50.3	0.1
Astronia williamsii	7.1	0.1
Evodia acuminata	7.1	0.1
Lisianthus chinensis	3.1	0.1
Podocarpus rotundus	19.6	0.1
Rapanea philippinensis	33.2	0.1
Unidentified	1,890.7	0.6
All species	70,827.7	25.7

Table 2. Density (number/m²) of leaf-litter and soil invertebrates sampled monthly in the mossy forest on Mt. Isarog, 1550 m.

Class/Order	Month					Mean ± SD
	Dec	Jan	Feb	Mar	Apr	
Annelida	11	29	45	35	28	30 ± 12.4
Crustacea						
Amphipoda	238	150	111	78	109	137 ± 61.9
Isopoda	32	25	25	18	23	25 ± 5.0
Chilopoda	11	19	17	60	3	22 ± 22.1
Diplopoda	30	47	88	36	62	53 ± 23.2
Arachnida						
Araneae	17	27	28	23	17	22 ± 5.3
Opiliones	2	5	8	3	0	4 ± 3.0
Pseudoscorpiones	0	0	2	0	0	—
Insecta[a]	74	54	53	14	24	44 ± 24.4
Total	415	356	377	267	266	336 ± 67.0

[a] Samples of Coleoptera, Diptera, Lepidoptera, and unidentified insects include larvae and pupae.

specimens deposited in the Field Museum and the American Museum of Natural History.

Apparently, Rabor did not make an intensive or systematic survey of small mammals on Mount Isarog. We are therefore unable to make a detailed comparison of the changes in the composition of small mammal communities in the ensuing 20 years, as was done for birds by Goodman and Gonzales (1990). A description of habitats is lacking, but we surmise that the vegetation in Rabor's study sites listed below approximated our present study sites at 300–900 m (his Sites 19–22, our Sites 1, 2, 12, and 13) and at 1750 m (his Site 23, our Sites 6, 17, and 18) in terms of forest structure. The degree of disturbance to forest at his lowland sites in 1961 was quite likely to have been less severe than that at our sites in 1988–1995. Locations plotted in Figure 5 are estimates based on elevation and specimen labels that state the localities were "above Curry."

Site 19—ca. 450 m (10 April 1961).

Site 20—ca. 600 m (12 April 1961).

Site 21—ca. 725 m (30 March; 3, 9, and 14 April 1961).

Site 22—ca. 800 m (7, 15, 23, and 25 April 1961).

Site 23—ca. 1700+ m (15, 25–28 April 1961).

Methods

Our studies in 1988 followed methods used in earlier studies on Leyte, Negros, Catanduanes, and other islands (Heaney et al., 1989, 1991;

Table 3. Biomass (mg/m²) of leaf-litter and soil invertebrates sampled monthly in the mossy forest on Mt. Isarog, 1550 m. Weights taken from drained fluid specimens.

Class/Order	Month					Mean ± SD
	Dec	Jan	Feb	Mar	Apr	
Annelida	1,024	2,155	2,348	6,401	4,461	3,278 ± 2,142.4
Crustacea						
Amphipoda	1,666	1,277	1,119	1,064	1,175	1,250 ± 240.3
Isopoda	304	265	334	267	307	295 ± 29.3
Chilopoda	149	196	270	60	33	142 ± 97.4
Diplopoda	339	399	541	942	1,027	650 ± 315.8
Arachnida						
Araneae	162	603	342	314	392	363 ± 159.4
Opiliones	1	33	33	68	0	27 ± 28.1
Insecta[a]	200	127	481	143	271	243 ± 144.3
Total	3,845	5,055	5,468	9,256	7,666	6,258 ± 2,171.6

[a] Includes all orders listed in Table 2.

Rickart et al., 1991) to facilitate comparisons. Bats were caught in mist nets set on ridgetops, across trails and streams, and at the edges of clearings adjacent to forest. Nets were tended continuously during the old-growth activity peak from early dusk (about 17:30) until about 21:00, and some were tended longer. Nets were left open thereafter, and bats were removed at dawn. Any given net was left in place for 3 or 4 days at a time in all but a few instances. We also captured *Megaderma spasma* from a roost in a hollow tree using a fragment of a mist net.

During 1988, nonvolant small mammals were caught in a mixture of Victor rat traps (ca. 75%) and National live traps (ca. 25%). Traps were baited late each afternoon with fresh fried coconut coated with peanut butter, or with live earthworms. Traps were checked each morning soon after dawn and late each afternoon, and occasionally in the early afternoon and evening. Traps were placed 5–15 m apart; most (95%) were placed on the ground, but ca. 5% were placed aboveground on fallen trees, horizontal branches, or large vines. Traps were left in place for 3–5 days but usually for 4 days.

The study conducted in 1989–1990 on the southern side of Mount Isarog (Ocampo Municipality) consisted of mist-netting and livetrapping. Mist nets were examined in the late afternoon and at dawn, and occasionally during the evening. We also captured *Emballonura alecto* in a cave and in several tunnels by setting mist nets at the entrances. Our record of *Pteropus hypomelanus* was of an individual shot by a local resident. We employed cage traps constructed from welded wire and baited with roasted coconut coated with peanut butter to capture nonvolant small mammals. At Sites 16 and 17, we used dried squid on some of the traps. When we returned to Site 17 in 1992, we used only Victor rat traps baited with earthworms.

From November 1993 to May 1994, a capture–mark–recapture study was conducted in the mossy forest at Site 18 (Balete, 1995; Balete & Heaney, 1997). From December 1993 to early February 1994, trapping was done on four 6 × 6 subgrids with an intertrap distance of 5 m for 4 days every other week using cage traps manufactured from welded wire. From late February to April, the intertrap distance was doubled to 10 m. Two types of baits were used: roasted strips of coconut coated with peanut butter during the first 2 days and live earthworms tied to the traps' bait hooks during the last 2 days.

During the final phase, sampling of nonvolant small mammals for stomach content analysis was done at 1500 and 1700 m using Victor rat traps baited with roasted coconut coated with peanut butter during the first 2 days and with live earthworms during the succeeding 2 days. Temperatures were recorded daily with minimum–maximum thermometers that were maintained in shaded spots about 1.5 m above the forest floor. Precipitation was measured with a rain gauge placed in a spot below an opening in the canopy. Further details on the methodology of this study were presented by Balete (1995) and Balete and Heaney (1997).

Unfortunately, we have no way to ascertain the specific collection techniques used by Rabor's field crews, but they probably included snap traps, mist nets, firearms, and acquisition from local hunters (Goodman & Gonzales, 1990).

Voucher specimens were prepared in fluid, as skeletons, or as skins with partial skeletons and have been deposited at the Field Museum, Chicago (FMNH), the Natural Science Museum at the Iligan Institute of Technology of Mindanao State University, Iligan City (NSM-IIT), the Philippine National Museum, Manila (PNM), University of the Philippines, Los Banos (UPLB), and the United States National Museum of Natural History, Washington, D.C. (USNM). Other specimens examined in the course of this study are deposited at the American Museum of Natural History (AMNH) and the Florida Museum of Natural History (FSM). In 1988, specimens were necropsied in the field for reproductive information. Size of embryos was measured as crown–rump length (CRL). Subadult animals are defined here as those that have not completed cranial growth, especially those having unfused basicranial sutures. Subadults lack adult pelage but are nearly as large as adults, and female subadults are often undergoing their first reproductive activity. Comments on distribution and use of scientific names are based on Heaney et al. (1998) unless stated otherwise. Records of specimens examined, including site number and number of specimens (in parentheses), are summarized at the end of each account.

External measurements and weights reported here were taken by the authors in the field on fresh animals in 1988. All cranial measurements were taken by Heaney with digital calipers graduated to 0.01 mm. Comparisons of cranial measurements that are made in this paper are to published records of specimens also measured by Heaney.

FIG. 11. Adult *Crocidura grayi*. 29 March 1988, at Site 3. L. R. Heaney.

In May 1990, the Wildlife Biology Laboratory at UPLB, where most of the specimens collected from the southern slope were deposited, was destroyed by fire. All specimens indicated as deposited at UPLB were lost during that fire and are presented here for the purpose of species accounts. Measurements taken from these specimens are not included in the computation of means and ranges of cranial and external measurements. Instead, such measurements, in the absence of other measurements from extant specimens of species from previous or later studies, are indicated in their respective species accounts.

Accounts of Species

Order Insectivora

Family Soricidae—Shrews

Crocidura grayi Dobson, 1890

Prior to this study, the Luzon white-toothed shrew (Fig. 11) had been reported from Catanduanes, northern Luzon, and Mindoro (Heaney et al., 1991; Heaney & Ruedi, 1994). This small shrew (10.8 g) was present from 475 m to 1750 m (Fig. 12) in disturbed and old-growth lowland forest and old-growth montane and old-growth mossy forest; it was significantly more abundant in montane forest than elsewhere (Rickart et al., 1991). A closely related species, *C. beatus,* showed similar patterns of elevational range and abundance on Leyte (Heaney et al., 1989; Rickart et al., 1993). Trap success for this species in 1988 ranged from 0.15% to 1.04% with coconut bait and from 0.29% to 2.91% with live earthworm bait; overall trap success was significantly greater with earthworm bait (χ^2 = 13.470; P < 0.001). Stomachs of snap-trapped specimens contained fragments of insects and terrestrial amphipods (amphipods were common at high elevations; Tables 2 and 3) but did not contain recognizable plant material (Rickart et al., 1991). This species is best described as a generalist insectivore.

Shrews were active both day and night; out of a total of 38 trapped specimens, 15 (39.5%) were taken during daylight hours. Three additional specimens were hand-caught during the day, and several others were sighted as they ran about the

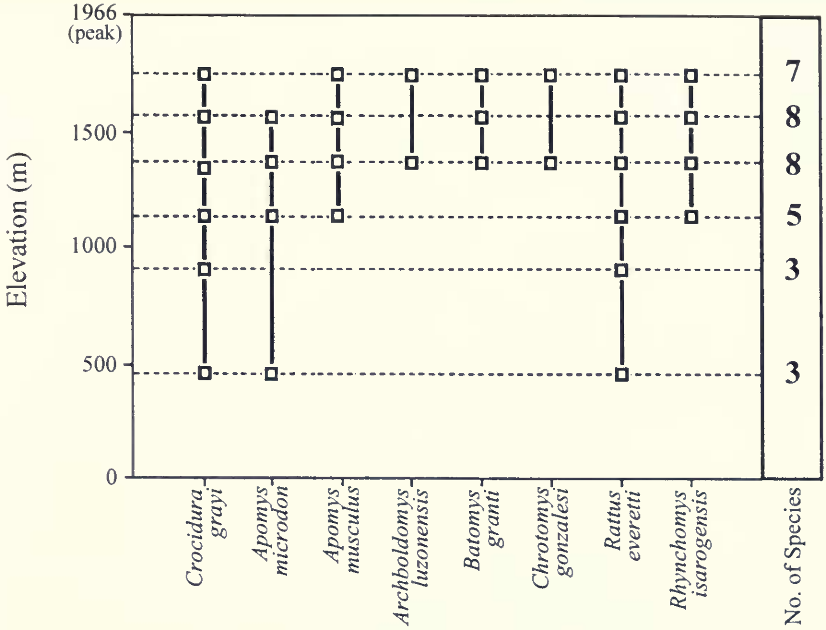

FIG. 12. Elevational distribution of native shrews and murid rodents on Mount Isarog. Numbers in the right column indicate the number of species known to be present at a given elevation and those inferred to be present because they were taken both above and below in the 1988 transect study. Dotted lines indicate the elevation of intensive sampling sites.

forest floor. All specimens were taken at the ground surface in areas of moderate to heavy cover, most often along runways next to fallen logs or at openings to tunnels along the steep sides of ravines or at the bases of live trees or stumps. The scats of viverrids collected by Balete (1995) did not reveal any indication of predation on this species (see *P. hermaphroditus* account, below).

Seventeen females were caught in March and April 1988. Of nine adults (10.3 ± 1.87 g) with enlarged mammae, four had a single embryo each and one had two embryos (CRL = 2–8 mm). Average litter size for eight females (based on counts of fetuses or placental scars) was 1.2 ± 0.5 (range, 1–2). Two adult females captured in April 1994 also had enlarged mammae; one had a swollen reproductive tract and the other had a single embryo (CRL = 7 mm). Testes of most males were abdominal. Testes size of seven adult males (11.1 ± 0.90 g) ranged from 2.5 × 3 mm to 3 × 4 mm. Nine other males of unverified age (9.6 ± 2.60 g) had testes size from 1.5 × 2 mm to 2.5 × 4.5 mm. See Heaney and Ruedi (1994) for cranial measurements.

SPECIMENS EXAMINED—Total 42. Site 1 (1 PNM); Site 2 (2 USNM); Site 3 (25 USNM); Site 4 (3 USNM); Site 5 (2 USNM); Site 6 (6 USNM); Site 18 (2 FMNH).

Suncus murinus (Linnaeus, 1766)

Our record of the Asian house shrew, a common non-native species, consisted of a single adult female. It was caught by a house cat in an agricultural area close to second-growth forest, at ca. 325 m, probably within or just outside a house. We trapped none within the forest, despite intensive sampling. Total length = 194 mm, tail length = 66 mm, hind foot = 18 mm.

SPECIMENS EXAMINED—Total 1. Site 8 (1 UPLB).

Order Chiroptera

Family Pteropodidae—Fruit Bats

Cynopterus brachyotis (Müller, 1838)

The common short-nosed fruit bat is widespread in Southeast Asia and is found on virtually every island in the Philippines, where it is abundant in agricultural areas and disturbed forests and often present but usually uncommon in old-growth lowland and montane rain forest (Heaney et al., 1989, 1991; Heideman & Heaney, 1989;

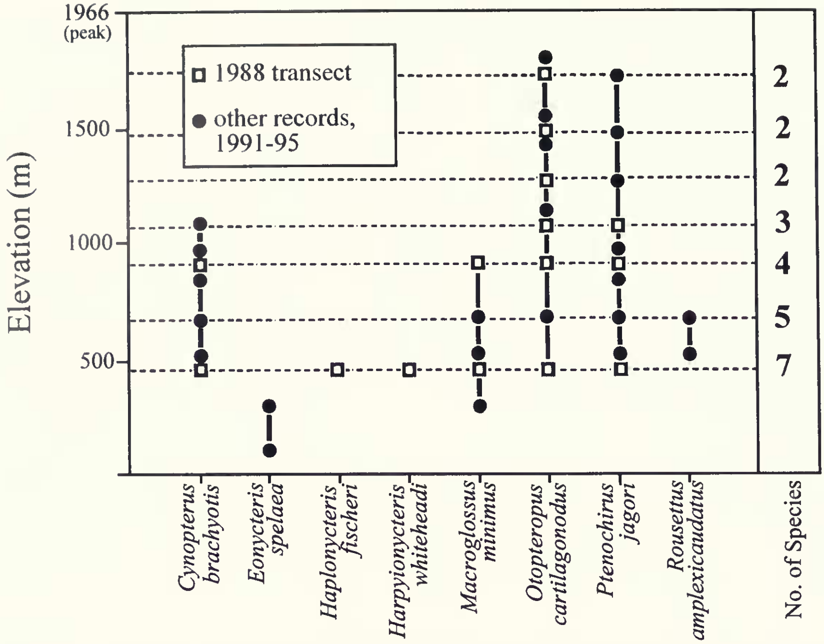

FIG. 13. Elevational distribution of fruit bats on Mount Isarog. Dotted lines indicate the elevation of intensive sampling sites.

Ingle, 1992; Lepiten, 1997; Rickart et al., 1993). Utzurrum (1992) considered Philippine populations to be stable or increasing and to be an important contributor to seed dispersal and natural forest regeneration in degraded habitats. This species is called *sabolo* by native settlers in Del Rosario, who sometimes hunt it for food. An indigenous contraption consisting of several thorny tips of rattan fronds, ca. 30 cm in length, tied together around one end of a long bamboo pole was used for catching these bats. The pole is used by the hunter to swat the bats attracted to fruiting or flowering trees. Those bats whose wings are caught in the thorny tips of the pole cannot free themselves.

Cynopterus brachyotis was abundant in disturbed forest at 475 m and in mixed second-growth and old-growth lowland forest at 900 m during our 1988 transect study but was not found at higher elevations (Fig. 13, Table 4). In 1989–

TABLE 4. Abundance and elevational distribution of fruit bats (Pteropodidae) on Mt. Isarog during 1988 field season. Data are from standardized sampling procedures.

	Sites and elevation (m)					
Species	1 475	2 900	3 1125	4 1350	5 1550	6 1750
Cynopterus brachyotis	67	20	0	0	0	0
Haplonycteris fischeri	4	0	0	0	0	0
Harpyionycteris whiteheadi	3	0	0	0	0	0
Macroglossus minimus	7	15	0	0	0	0
Otopteropus cartilagonodus	16	25	5	5	1	1
Ptenochirus jagori	17	18	3	0	0	0
Total species	6	4	2	1	1	1
Total bats	113	76	8	5	1	1
Total net-nights	75	54	56	63	66	26
Species/net-night	0.08	0.07	0.04	0.02	0.02	0.04
Fruit bats/net-night	1.51	1.41	0.14	0.08	0.02	0.04

FIG. 14. *Cynopterus brachyotis* roosting in a palm leaf that has been modified into a "tent." April 1992, Del Rosario, Ocampo Municipality. D. S. Balete.

1990, along the southern transect, they were common in agricultural areas, second-growth, and disturbed forest from 500 to 1100 m but were absent in old-growth forest at higher elevations where *Otopteropus cartilagonodus* predominated.

Thirteen primiparous females (28 ± 1.6 g) and 18 multiparous females (31 ± 1.9 g) each were pregnant with a single embryo (CRL = 10.4 ± 4.5 mm). Two multiparous females (38 g each) captured in May 1988 were pregnant with single embryos (CRL = 27 and 39 mm). Testes of males netted in March 1988 ranged from 2 × 3 mm to 5 × 6 mm. Males with full adult pelage averaged 30.6 g (range = 25–36 g, N = 24), and those with the dull subadult pelage averaged 26.6 g (range = 22–32 g, N = 6). Reproductive patterns in this species were described by Heideman (1995).

In an agricultural area at Del Rosario, near Site 8, in April 1992, we observed *C. brachyotis* roosting singly and in groups of up to four individuals in tent roosts constructed from the large circular leaves of anahaw palm (*Livistona* sp.) in a fashion similar to that described by Utzurrum (1992) for *C. brachyotis* in Manila and by Rickart et al. (1989) for *Scotophilus kuhlii* in Quezon City. Two palm trees each had five leaves turned into tent roosts, but most were not occupied when the observation was made. Close examination of the tent roosts revealed that they were all formed by chewing roughly 3-cm segments of almost all of the midribs of the deeply lobed, circular palm leaf. The leaf then drooped from the ends of the chewed parts, forming an umbrella-shaped structure. Chewed midribs formed a circular shape with a radius of ca. 15 cm from the distal end of the leaf petiole (Fig. 14). In December 1993, shortly after a typhoon struck the area, we observed two *C. brachyotis* roosting under the fronds of tree ferns.

Measurements are given in Table 5. Cranial variation throughout the Philippines (Biliran, Camiguin, Catanduanes, Leyte, Luzon, Maripipi, and Negros) appears to be slight (Heaney, 1984; Heaney et al., 1991; Heaney & Rabor, 1982; Rickart et al., 1993), and analysis of variation in allozymes indicated little genetic variation between Philippine populations (Peterson & Heaney, 1993). Kitchener and Maharadatunkamsi (1991) and Schmitt et al. (1995) have suggested that *C. b. luzoniensis* from the Philippines and Sulawesi

TABLE 5. Mean (± SD) and range of selected cranial and external measurements of adult fruit bats (Pteropodidae) from Mt. Isarog, southern Luzon, Philippines. Sample size other than N is indicated by the number enclosed in parentheses after the range. Measurements taken from sample sizes of 2 and 3 are given as averages and their ranges. All measurements except weight are in millimeters.

Species	Sex	N	Condylo-basal length	Zygomatic breadth	Inter-orbital width	Post-orbital width	Mastoid breadth
Cynopterus brachyotis	M	10	28.4 ± 0.81	18.9 ± 0.65	6.5 ± 0.34	6.5 ± 0.61	12.0 ± 0.44
			27.0–29.4	17.7–19.8	6.0–7.0	5.7–7.3	11.4–12.6
	F	10	27.9 ± 0.65	18.6 ± 0.40	6.3 ± 0.29	6.5 ± 0.31	11.8 ± 0.39
			26.6–29.1	18.0–19.2	5.9–6.6	6.2–7.0	11.1–12.4
Haplonycteris fischeri	M	3	23.7	16.4	6.0	6.3	10.6
			23.2–24.1	15.8–17.2	5.8–6.2	6.1–6.4	10.4–10.9
	F	1	23.4	16.4	5.5	4.9	10.3
Harpyionycteris whiteheadi	M	1	40.7	23.8	6.7	6.6	15.1
Macroglossus minimus	M	6	24.1 ± 0.54	14.0 ± 0.70	4.7 ± 0.27	7.0 ± 0.30	9.9 ± 0.34
			23.2–24.8	13.1–14.6	4.3–5.1	6.6–7.4	9.4–10.3
	F	8	24.3 ± 0.65	13.3 ± 0.33	4.6 ± 0.16	7.0 ± 0.17	9.8 ± 0.16
			23.3–25.2	12.8–13.6	4.4–4.9	6.7–7.2	9.5–10.0
Otopteropus cartilagonodus	M	6	22.3 ± 0.41	15.0 ± 0.56	3.7 ± 0.28	6.2 ± 0.40	10.0 ± 0.12
			21.8–22.9	14.2–15.5	3.4–4.1	5.6–6.6	9.9–10.2
	F	7	22.4 ± 0.36	15.1 ± 0.31	3.8 ± 0.29	6.4 ± 0.21	10.0 ± 0.23
			21.8–22.9	14.6–15.4	3.4–4.2	6.1–6.6	9.7–10.4
Ptenochirus jagori	M	7	33.5 ± 1.06	23.8 ± 0.95	7.0 ± 0.49	6.2 ± 0.27	14.2 ± 0.37
			32.1–35.1	22.5–25.5	6.6–8.1	5.9–6.6	13.6–14.6
	F	10	33.4 ± 0.87	23.5 ± 0.97	6.9 ± 0.38	6.4 ± 0.22	14.3 ± 0.44
			32.1–34.9	21.9–24.9	6.2–7.3	6.2–6.8	13.5–14.9
Pteropus hypomelanus	F	1	—	33.6	8.4	9.1	19.5

be recognized as a distinct species. However, they included too few localities and specimens to document the patterns of geographic variation within the Philippines, and we recommend further study before their recommendations are accepted.

SPECIMENS EXAMINED—Total 115. Site 1 (17 PNM, 59 USNM); Site 2 (20 USNM); Site 9 (4 UPLB); Site 12 (5 UPLB); Site 13 (7 UPLB); Site 14 (3 UPLB).

Eonycteris spelaea (Dobson, 1871)

The cave-roosting nectar bat is strongly associated with lowland agricultural areas (Heaney et al. 1989; Heideman & Heaney, 1989). We netted only two specimens, in agricultural areas at 100 and 300 m elevation (Fig. 8) in Ocampo Municipality. Ingle (1992) netted only six among over 1,500 bats captured in lowland forest at 200–500 m elevation on Mount Makiling. Although we found this species to be uncommon on Mount Isarog, it is believed to have generally stable or increasing populations in the Philippines (Utzurrum, 1992), though individuals may be subject to intensive human hunting in the caves where they roost (e.g., on Leyte; Rickart et al., 1993).

SPECIMENS EXAMINED—Total 2. Site 7 (1 UPLB); Site 8 (1 UPLB).

Haplonycteris fischeri Lawrence, 1939

The Philippine pygmy fruit bat, a widespread Philippine endemic, is often common in old-growth forests, especially in montane forest; it is rarely present in agricultural land and is uncommon in second-growth forests (Heaney et al., 1989, 1998; Heideman & Heaney, 1989; Rickart et al., 1993). Utzurrum (1992) considered the species to be widespread and stable in numbers but vulnerable to habitat destruction. We netted only five individuals, all adults, in disturbed lowland forest at the 475 m site and none in old-growth forest at higher elevations (Fig. 13, Table 4). Heaney et al. (1991) found them to be common in lowland forest on Catanduanes, Ingle (1992) captured 14 at 200–500 m elevation on Mount Makiling, Laguna Province, and Ruedas et al. (1994) captured only one, at 1100 m, in Zambales Province, west-central Luzon. These observations may imply that this species has a lower elevational range in the Greater Luzon area (e.g., Ingle, 1993) than in the central Philippines, where previous studies have

TABLE 5. *Extended.*

Rostral length	Orbital length	Post-orbital length	C to last M	Molariform tooth row	Palatal breadth at last M	Palatal length	Total length
9.2 ± 0.44	12.0 ± 0.39	13.4 ± 0.46	9.6 ± 0.33	6.7 ± 0.23	6.2 ± 0.25	14.4 ± 0.35	100 ± 4.7
8.5–9.7	11.5–12.7	12.6–14.2	8.8–10.1	6.3–7.1	5.8–6.5	13.6–14.8	94–115 (21)
9.0 ± 0.33	11.6 ± 0.37	13.1 ± 0.43	9.6 ± 0.14	6.7 ± 0.16	6.3 ± 0.27	13.9 ± 0.33	100 ± 4.8
8.5–9.5	11.2–12.3	12.5–13.7	9.4–9.9	6.5–7.1	5.9–6.7	13.3–14.3	92–118 (40)
7.8	9.5	11.9	8.5	6.0	4.9	11.5	71.3
7.5–8.1	9.4–9.8	11.7–12.2	8.3–8.7	5.9–6.1	4.7–5.0	11.3–11.7	70–73
7.7	9.3	11.4	8.2	5.7	4.9	11.2	73
11.4	17.9	15.2	15.6	11.5	7.9	20.1	140
9.0 ± 0.28	7.9 ± 0.33	10.5 ± 0.15	8.3 ± 0.34	5.1 ± 0.23	4.9 ± 0.21	12.8 ± 0.36	70 ± 5.0
8.6–9.3	7.4–8.3	10.3–10.7	7.9–8.8	4.8–5.4	4.6–5.1	12.2–13.3	65–77
9.3 ± 0.41	7.8 ± 0.31	10.2 ± 0.19	8.6 ± 0.26	5.3 ± 0.20	5.1 ± 0.20	13.2 ± 0.37	70 ± 4.1
8.7–9.9	7.4–8.2	9.9–10.4	8.3–9.0	5.0–5.6	4.7–5.3	12.7–13.8	65–77 (9)
7.4 ± 0.27	8.9 ± 0.21	10.6 ± 0.10	7.4 ± 0.17	5.1 ± 0.12	4.7 ± 0.19	11.2 ± 0.39	73 ± 5.4
6.9–7.6	8.6–9.2	10.4–10.7	7.2–7.7	5.0–5.3	4.5–5.0	10.7–11.8	65–79 (9)
7.5 ± 0.29	8.9 ± 0.33	10.9 ± 0.30	7.4 ± 0.14	5.1 ± 0.13	4.9 ± 0.18	11.3 ± 0.28	75 ± 4.9
7.1–7.8	8.4–9.3	10.5–11.4	7.1–7.5	4.9–5.3	4.7–5.2	10.8–11.7	66–83 (23)
10.4 ± 0.40	15.1 ± 0.55	15.8 ± 0.52	11.8 ± 0.49	8.4 ± 0.35	7.6 ± 0.22	16.8 ± 0.71	125 ± 7.6
9.9–11.2	14.4–16.1	14.9–16.4	11.3–12.8	8.2–9.0	7.3–8.0	15.8–18.1	113–146 (17)
10.2 ± 0.52	15.3 ± 0.57	15.7 ± 0.43	11.6 ± 0.26	8.4 ± 0.22	7.7 ± 0.34	16.8 ± 0.60	126 ± 5.6
9.5–11.0	14.3–16.0	15.1–16.3	11.2–12.0	8.1–8.7	7.2–8.1	15.5–17.7	117–138 (13)
21.6	23.9	—	21.9	16.0	11.8	33.2	—

been done (e.g., Heaney et al., 1989; Rickart et al., 1993). This species feeds heavily on the fruits of wild fig trees (*Ficus* spp.; Utzurrum, 1995). We caught most of our specimens at Site 1 in a location where fruiting fig trees were abundant in second growth under the canopy of the introduced *Leucaena leucocephala.*

Three males (16–18 g, N = 2) netted in March 1988 had testes measuring 4 × 4 mm to 5 × 6 mm. A multiparous female (17 g) with enlarged mammae had a single embryo (CRL = 2 mm). This species has delayed development and highly synchronous reproductive cycles within populations (Heideman, 1988, 1989).

Cranial measurements (Table 5) are similar to those of series from Biliran, Catanduanes, Dinagat, Leyte, Luzon, and Negros; cranial geographic variation appears to be slight (Heaney, 1984; Heaney & Rabor, 1982; Heaney et al., 1991; Rickart et al., 1993). Genetic geographic variation in the species is substantial and is associated principally with the extent of Pleistocene islands (Peterson & Heaney, 1993).

SPECIMENS EXAMINED—Total 5. Site 1 (1 PNM, 4 USNM).

Harpyionycteris whiteheadi Thomas, 1896

The Philippine harpy fruit bat, an endemic species, was unknown from Luzon Island prior to our study; previous records were from Camiguin, Mindoro, Negros, and several islands of Greater Mindanao (Biliran, Leyte, Maripipi, and Mindanao; Heaney, 1991; Peterson & Fenton, 1970; Rickart et al., 1993). The three specimens reported here constitute the first record from Greater Luzon and formed the basis for the inclusion of this species in the Luzon fauna by Heaney (1991) and Heaney et al. (1998). The species is common in old-growth mid-elevation forest on Leyte and Negros, occasionally venturing into adjacent second-growth forest (Heaney et al., 1989; Heideman & Heaney, 1989; Rickart et al., 1993). Utzurrum (1992) considered this species to have stable populations but to be vulnerable to habitat destruction, and noted that they typically occur in low densities.

On the evening of 4 May 1988, we heard the penetrating whistling call of this species along a ridgetop in mixed agricultural land and second growth forest at 475 m (Site 1). We traced the

TABLE 5. *Extended.*

Species	Tail length	Hind foot	Ear	Forearm	Weight (g)
Cynopterus brachyotis	7 ± 2.8	16.3 ± 1.3	18 ± 1.2	63 ± 2.8	29.5 ± 2.63
	2–12 (21)	13–17 (18)	15–20 (21)	58–70 (21)	24.5–35 (21)
	8 ± 2.1	16 ± 1.0	18 ± 1.0	62.4 ± 2.02	29.7 ± 2.58
	3–12 (39)	13–18 (36)	15–19 (40)	58–68 (40)	25.5–38 (39)
Haplonycteris fischeri	0	12.8	14.0	46.3	17.0
	—	12–13	13–15	42–50	16–18(2)
	0	13	13	50	17
Harpyionycteris whiteheadi	0	23	23	85	102
Macroglossus minimus	0	15 ± 3.0	16 ± 0.8	42 ± 1.5	13.6 ± 0.74
	—	12–18	15–17	39–43	12.5–14.5
	0	13 ± 2.0	16 ± 0.9	42 ± 0.8	14.8 ± 2.67
	—	12–17 (9)	14–17 (9)	41–43 (9)	11.5–21 (9)
Otopteropus cartilagonodus	0	13 ± 3.0	13 ± 0.9	48 ± 1.3	16.5 ± 1.59
	—	11–19 (9)	12–14 (9)	46–51 (9)	15–20 (9)
	0	14 ± 3.0	14 ± 0.7	48.3 ± 1.65	15.9 ± 1.73
	—	11–19 (23)	12–15 (23)	44–52 (23)	13–19 (23)
Ptenochirus jagori	11 ± 2.4	20 ± 1.2	20 ± 1.1	78 ± 3.5	62.9 ± 7.10
	6–14 (16)	19–22 (12)	18–23 (17)	72–84 (17)	45–73 (17)
	9 ± 2.7	22 ± 0.8	20 ± 0.9	77 ± 3.2	66.5 ± 10.41
	4–14 (12)	21–23 (13)	18–21 (13)	73–83 (13)	55–87 (13)
Pteropus hypomelanus	—	—	—	—	—

calls to a fruiting pandan vine (*Freycinetia* sp.) in a large tree, where we saw the bats land and feed on the fruits. On that and the following night we saw many *H. whiteheadi* feeding on the fruit of the same vine, and we netted three males, an adult (102 g), a subadult (83 g), and a juvenile (77 g). We had heard the calls of this species in the same area in April 1988. The limited available evidence indicates that viney pandans (*Freycinetia* spp.) form the old-growth food for this species (Utzurrum, 1995). Reproductive patterns in this species were described by Heideman (1995).

Cranial measurements of the single adult male (Table 5) fit well within the range of those from Leyte (Rickart et al., 1993) but are slightly smaller than those of several specimens from Camiguin (Heaney, 1984). Assignment to subspecies as defined by Peterson and Fenton (1970) seems ambiguous; geographic variation needs to be reassessed.

SPECIMENS EXAMINED—Total 3. Site 1 (3 USNM).

Macroglossus minimus (E. Goeffroy, 1810)

The dagger-toothed flower bat is found from Thailand to Australia (Koopman, 1993); in the Philippines it is abundant in agricultural areas on most islands (Heaney, 1991; Heaney et al., 1998). Utzurrum (1992) considered it to have generally stable or increasing populations in the Philippines. It is found at virtually all elevations where *Musa* (banana and abaca) is present, though usually in higher density at low than at high elevation (Heaney et al., 1989; Heideman & Heaney, 1989; Ingle, 1992; Lepiten, 1997; Rickart et al., 1993).

On Mount Isarog, these small bats were common in habitats ranging from 300 to 900 m (Fig. 13) in mixed agricultural land and remnant forest (Sites 8 and 9), disturbed forest adjacent to agricultural land (Sites 1 and 12), and mixed old-growth lowland forest and agricultural land (Site 2; Table 4). In most places they were associated with domestic or wild banana. Local farmers and workers in abaca plantations told us that this species often roosts under dried, drooping leaves of abaca and banana.

Eight multiparous (15 ± 3.0 g) and three primiparous (13, 14, and 15 g) females netted in March 1988 were pregnant, each with a single embryo (CRL = 8 ± 6.5 mm). Seven adult males weighed 14 ± 0.8 g; three were noted as having abdominal testes (2 × 3 mm to 7 × 8 mm).

SPECIMENS EXAMINED—Total 26. Site 1 (1 PNM, 7 USNM); Site 2 (13 USNM); Site 8 (1 UPLB); Site 9 (3 UPLB); Site 12 (1 UPLB).

FIG. 15. *Otopteropus cartilagonodus*. 27 March 1988, Site 3, L. R. Heaney.

Otopteropus cartilagonodus Kock, 1969

Prior to our 1988 survey, the Luzon pygmy fruit bat (Fig. 15), a poorly known Luzon endemic, was reported only from northern Luzon (Heaney et al., 1998; Kock, 1969; Mudar & Allen, 1986). Ingle (1992) took none in over 1,500 bats captured in lowland forest at 200–500 m elevation on Mount Makiling, Laguna Province. Ruedas et al. (1994) reported on specimens from Zambales Province, Luzon, and included those described here. Utzurrum (1992) described this species as having stable populations but being vulnerable to habitat destruction because of the apparent restriction to old-growth or lightly disturbed forest.

We found this species throughout our netting transects, from 475 m to 1750 m and above (Fig. 13); it was either the most common or the only fruit bat at all sites except Site 1 (475 m), where *Cynopterus brachyotis* was most common (Table 4). Along the western transect, it was common in mixed secondary and old-growth lowland forest and agricultural land at 475 m and 900 m sites (Table 4) and uncommon at higher elevations. On the southern transect, we found it to be common in old-growth upper montane and transitional montane–mossy forest at 1300–1500 m. As noted by Ruedas et al. (1994), we found males to be proportionately more numerous than females at higher elevations and females to predominate at lower elevations. Seasonal variation in habitat use is unknown.

A subadult (14.5 g) and five adult (16.8 ± 2.14 g) females were netted in January 1990 at Site 15. In March 1988, all of the 33 females we netted, consisting of 15 adults (15.6 ± 1.16 g, N = 14), 5 young adults (14.5 ± 1.3 g), and 13 of undetermined age, each had a single embryo (CRL = 2.5 ± 0.46 mm, N = 31). Each of the four multiparous females (18 ± 1.0 g) netted in May 1988 also had a single but larger embryo (CRL = 14 ± 1.3 mm). Twenty-eight males were netted in December 1989 and January 1990 at Sites 15–17, of which 14 adults weighed 18.0 ± 1.56 g and 2 subadults weighed 13 and 15.5 g. Six adult (17.2 ± 1.57 g) and three young adult (15, 15, and 16.5 g) males captured in March and May had small testes ranging in size from 1 × 2 mm to 3 × 4 mm. On the basis of specimens collected in 1988, Heideman et al. (1993) suggested that this species exhibits highly synchronized annual reproduction and delayed development, a pattern also found in

Haplonycteris fischeri (Heideman, 1989). Measurements are provided in Table 5 and in Ruedas et al. (1994).

SPECIMENS EXAMINED—Total 88. Site 1 (1 FMNH, 2 PNM, 13 USNM); Site 2 (2 PNM, 23 USNM); Site 3 (2 PNM, 5 USNM); Site 4 (1 FMNH, 3 USNM); Site 5 (1 USNM); Site 6 (1 USNM); Site 12 (1 UPLB); Site 15 (1 FMNH, 1 IITM, 20 UPLB); Site 16 (6 UPLB); Site 17 (5 UPLB).

Ptenochirus jagori (Peters, 1861)

The musky fruit bat, an endemic Philippine species, is found throughout the Philippines except the Palawan and Batanes/Babuyan regions. It is common in old-growth and lightly disturbed forest and sometimes is present in more degraded forest (Heaney et al., 1998; Heideman & Heaney, 1989; Lepiten, 1997; Rickart et al., 1993). It was the most abundant species of fruit bat (80% of 1,430 captures) in lightly disturbed forest at 200–500 m elevation on Mount Makiling, Laguna Province (Ingle, 1992). These bats feed principally on fruit of wild figs (*Ficus* spp.; Utzurrum, 1995). Utzurrum (1992) considered them to have generally stable populations but to be vulnerable to habitat destruction because of their dependence on low-elevation rain forest.

Along our western transect on Mount Isarog, this species was common in disturbed lowland forest (475 and 900 m), uncommon in lower montane forest at 1125 m, and absent at higher elevations (Fig. 13, Table 4). It was found in a greater range of elevations and habitats along the southern transect, from heavily disturbed lowland forest at 450 to mossy forest at 1750 m, but was most common in lowland and lower montane forest (Table 4). In January 1990, five individuals of this species were flushed from their roost under a large branch, ca. 15 m above ground, that was covered with epiphytes and a large bird's nest. The roost was found in old-growth montane forest at 1300 m at Site 15.

Eleven females (63 ± 7.1 g) were captured in May 1988; each had a single embryo (CRL = 2–8 mm). Two other pregnant females netted in May were heavier (68 and 87 g) and had larger embryos (CRL = 31 and 35 mm). Of 20 males netted in March 1988, 11 adults (65 ± 5.4 g) had larger testes (3 × 5 mm to 9 × 12 mm) than the 3 young adults (55, 61 and 64 g; testes size: 3 × 3, 4 × 4, 6 × 7 mm) and the 6 subadults (52 ± 3.7 g, testes size: 2 × 2 mm to 3 × 5 mm). An adult male (63 g) and a young adult male (61 g) captured in May 1988 had testes size of 6 × 8 mm and 6 × 7 mm, respectively. Reproductive patterns in this species were described by Heideman (1995) and Heideman and Powell (1998).

Geographic variation in this species is conspicuous. Cranial measurements of Mount Isarog bats (Table 5) are similar to those of bats from Catanduanes (Heaney et al., 1991) but are markedly smaller than those of bats from Biliran, Dinagat, Leyte, Maripipi, and Negros (Heaney & Rabor, 1982; Rickart et al., 1993); bats from Camiguin appear to be intermediate (Heaney, 1984).

SPECIMENS EXAMINED—Total 82. Site 1 (12 PNM, 22 USNM); Site 2 (4 PNM, 15 USNM); Site 3 (3 USNM); Site 9 (4 UPLB); Site 12 (1 UPLB); Site 13 (11 UPLB); Site 15 (6 UPLB); Site 16 (3 UPLB); Site 17 (1 UPLB).

Pteropus hypomelanus Temminck, 1853

The common island flying fox is distributed from the Maldive Islands to the Solomon Islands (Koopman, 1993) and is found through most of the Philippines, where it is common in lowland agricultural areas and often hunted for food (Heaney et al., 1998; Rickart et al., 1993). Utzurrum (1992) considered this species to have declined substantially in the Philippines in recent years but to be the least endangered of the Philippine flying foxes because of its wide range and the presence of populations in some protected areas.

Our only record of this species on Mount Isarog was a young adult female (261 g, forearm = 121 mm) shot by a local hunter in December 1989 among fruiting fig trees (*Ficus* spp.) in an agricultural area in Del Rosario at 400 m near Site 8; measurements are provided in Table 5. A single flying fox sighted on 5 March 1988 as it flew overhead at dusk may also have been this species. It is called *sabulaw* (= golden) by local hunters in reference to its golden mantle. Hunters in this area also described to one of us (D. S. Balete) at least two other flying foxes, which are reported below under *P. leucopterus* and *P. vampyrus*. Two more large bats known to the hunters as *paluypuyon* and *tarungan* were present; we suspect that these may be *Acerodon jubatus* and *Pteropus pumilus*, but further data are required to verify this identification.

SPECIMENS EXAMINED—Total 1. Site 8 (1 UPLB).

Pteropus leucopterus Temminck, 1853

The mottle-winged flying fox is a poorly known endemic species recorded only from Catanduanes (Heaney et al., 1991), Dinagat, and Luzon (Heaney & Rabor, 1982). Utzurrum (1992) considered the species to have declined substantially in recent years and to be in need of protection.

Although we captured none of these bats on Mount Isarog, reports from knowledgeable and apparently reliable local hunters lead us to believe that they are present. These hunters reported a bat they called *angaspa* and described it as larger than *P. hypomelanus* but with white wings. The hunters stated that these white-winged bats were particularly fond of feeding on the flowers of rarang, *Erythrina subumbrans,* when this tree begins to bloom, typically in February. It is said to be very aggressive and tends to drive away other flying foxes trying to feed on the same tree.

Pteropus vampyrus (Linnaeus, 1758)

The large flying fox occurs from Indochina to the Lesser Sunda Islands (Koopman, 1989, 1993). It is widespread in the Philippines (excluding the Batanes/Babuyan region), although it is intensively hunted in many areas and has declined substantially in numbers (Utzurrum, 1992).

A single specimen of this species was taken by the Rabor team on 23 April 1961; no elevation was noted, but other specimens taken on the same date were from ca. 800 m (Site 22). We neither saw nor captured any in 1988–1990, but in 1989–1990 local hunters on Mount Isarog reported to us a very large black bat, much larger than *P. hypomelanus,* which they called *dulom* (meaning pitch dark, as the ambient light during a new moon). This report seems to agree with the appearance of the common melanistic morph of *P. vampyrus.* These reports indicate that this species may have been present in low numbers during our studies.

Specimens Examined—Total 1. Pili, barangay Curry (1 amnh).

Rousettus amplexicaudatus (E. Geoffroy, 1810)

The common rousette ranges from Thailand to the Solomon Islands (Koopman, 1989, 1993). In most areas of the Philippines, it is among the most abundant species in agricultural areas, despite being hunted in the caves where it roosts (Heaney et al., 1989; Utzurrum, 1992). It is also sometimes present, but usually quite uncommon, in old-growth forest (Heideman & Heaney, 1989; Lepiten, 1995; Rickart et al., 1993). In November 1989, we netted two females, an adult with enlarged mammae (85.7 g) and a young adult (82.2 g), in heavily disturbed forest at ca. 500 m (Site 9) and 675 m (Site 12).

Specimens Examined—Total 2. Site 9 (1 uplb), Site 12 (1 uplb).

Family Emballonuridae—Sheath-tailed bats

Emballonura alecto (Eydoux and Gervais, 1863)

The Philippine sheath-tailed bat is known from Borneo and Sulawesi (Koopman, 1989, 1993) and is found virtually throughout the Philippines (Heaney et al., 1998). We captured two adult males in December 1987 in dimly lit areas in a shallow cave along Anangi Creek at 475 m (Site 10) in an abaca plantation with no intact forest around it. A few days later we captured four males and six females from a group of ca. 25 individuals inside a shallow tunnel along the Tabuan River in an area of mixed secondary forest and agricultural land at 475 m (Site 11). These sites are similar to the small caves surrounded by disturbed forest where these bats have been found on Catanduanes (Heaney et al., 1991), Leyte, and Maripipi (Rickart et al., 1993) and on Mount Makiling, Laguna Province, Luzon (Ingle, 1992). In December 1989, all of the six males (5.9 $\pm$ 0.38 g) we netted had abdominal testes, and five (5.9 $\pm$ 0.22 g) of the six adult females had enlarged mammae.

Two additional specimens were captured at Site 11 on 11 April 1994: a male (5 g) with undescended testes and a pregnant female (8 g) with a single embryo (CRL = 20 mm). The number of bats during this visit to the tunnel along the Tabuan River appeared to have increased to about 50 from the ca. 25 bats observed during our visit in December 1989. Two other caves along this river, which were uninhabited by this species in 1989, had small colonies of ca. 10–15 bats in April 1994. Measurements are given in Table 6.

Specimens Examined—Total 14. Site 10 (2 uplb); Site 11 (2 fmnh; 10 uplb).

TABLE 6. Mean (± SD) and range of selected cranial and external measurements of adult microbats (Emballonuridae, Megadermatidae, and Rhinolophidae) from Mt. Isarog, southern Luzon, Philippines. Sample size smaller than N is indicated by the number enclosed in parentheses after the range. Measurements taken from sample size of 2 are given as averages and their ranges. All measurements except weight are in millimeters.

Species	Sex	N	Condylo-incisive length	Zygomatic breadth	Inter-orbital width	Condylo-canine length	Mastoid breadth
Emballonura alecto	M	1	13.4	8.8	2.8	12.9	7.6
	F	1	13.8	9.1	2.9	13.2	7.8
Megaderma spasma	M	2	—	14.4	3.4	23.0	11.6
			—	14.4–14.5	3.3–3.4	22.7–23.4	11.6
	F	2	23.4	—	3.8	22.8	11.5
			23.2–23.7	14.9 (1)	3.8–3.9	22.4–23.1	11.4–11.6
Hipposideros bicolor[a]	M	1	16.2	8.8	2.6	15.2	9.0
Hipposideros diadema	F	3	25.6	16.6	3.4	25.7	13.8
			25.3–26.0	16.3–17.1	3.3–3.6	25.5–26.0	13.7–13.9
Hipposideros obscurus	M	1	16.4	10.9	2.3	16.3	9.6
Hipposideros pygmaeus	M[b]	5	12.3 ± 0.22	6.8 ± 0.13	2.0 ± 0.07	11.7 ± 0.34	6.9 ± 0.10
			12.3–12.4	6.8–6.9	1.9–2.0	11.7–12.0	6.9–7.0
Rhinolophus arcuatus-1	M	3	18.6	9.7	1.9	17.8	9.5
			18.3–19.0	9.4–9.9	1.8–2.0	17.6–18.0	9.2–9.7
	F	2	18.3	9.2	2.0	17.8	9.2
			17.8–18.8	9.0–9.4	1.8–2.1	17.6–18.0	9.1–9.4
Rhinolophus inops	M	3	22.9	12.0	2.1	17.4	11.3
			22.6–23.1	11.7–12.2	2.0–2.2	17.3–17.5	11.2–11.3

[a] External measurements taken on alcohol specimen.
[b] Includes two individuals of undetermined sex.

Family Megadermatidae—False vampire bats

Megaderma spasma (Linnaeus, 1758)

The common Asian ghost bat (or lesser false vampire bat) is a widespread species found from India to the Molucca Islands (Koopman, 1989, 1993); it occurs throughout the Philippines, except on the Batanes and Babuyan islands (Heaney et al., 1998). We netted individuals in old-growth and disturbed lowland forest at 475 and 900 m (Sites 1 and 2; Fig. 16); most other Philippine records are from lowland forest, although these bats occasionally are found in montane forest (Heaney et al., 1991; Lepiten, 1997; Rickart et al., 1993). Additionally, in March 1988 we found a colony of two females and three males roosting inside a hollow in a large strangler fig (*Ficus* sp.) in a clearing near Site 2 at ca. 800 m, less than 1 km away from disturbed old-growth forest. One female had large mammae, and both were pregnant with one embryo each of 12 mm and 14 mm CRL. Adult males had scrotal testes of 2 × 3 mm to 5 × 6 mm.

Cranial measurements of Mount Isarog specimens (Table 6) are nearly identical to those of bats from Catanduanes (Heaney et al., 1991) and Dinagat (Heaney & Rabor, 1982) but are slightly larger than those of specimens from Biliran, Leyte (Rickart et al., 1993), and Mindanao (Heaney & Rabor, 1982). Females appear to be consistently larger than males (Table 6; see also Heaney & Rabor, 1982; Heaney et al., 1991; Rickart et al., 1993).

SPECIMENS EXAMINED—Total 9. Site 1 (3 USNM); Site 2 (6 USNM).

Family Rhinolophidae—Horseshoe-nosed Bats

Hipposideros bicolor (Temminck, 1834)

The bicolored roundleaf bat has been recorded from India to Timor (Koopman, 1989, 1993); in the Philippines it is known from Luzon, Mindoro, and Palawan (Heaney et al., 1998). A single specimen (Table 6), taken on an unknown date near Pasacao on the Ragay Gulf coast ca. 40 km southwest of Mount Isarog (13°32′N, 123°03′E), is the sole record of this species in southern Luzon; Ruedas et al. (1994) reported one from Zambales Province in central Luzon. We captured none on Mount Isarog but suspect that this species once

Table 6. *Extended.*

Rostral length	Orbital length	CI to last M	Molariform tooth row	Palatal breadth at last M	Palatal length	Total length
3.3	5.6	5.4	3.9	3.3	4.8	57
3.4	5.5	5.6	4.1	3.3	4.8	63
5.2	7.8	9.1	7.0	3.6	6.9	74 ± 4.79
5.2	7.8	8.9–9.3	6.9–7.2	3.5–3.6	6.7–7.1	70–80 (4)
5.4	8.0	9.2	7.2	3.7	6.8	72
5.3–5.5	7.9–8.1	8.9–9.4	7.1–7.3	3.6–3.8	6.5–7.1	71–72
4.8	5.8	5.8	4.6	3.6	6.1	—
5.3	9.4	10.8	8.2	7.4	9.9	141
5.2–5.5	9.2–9.7	10.4–10.7	7.9–8.4	7.2–7.7	9.7–10.1	137–148
3.5	6.7	6.4	5.1	5.3	5.6	72
4.0 ± 0.14	3.9 ± 0.08	4.6 ± 0.09	3.6 ± 0.04	2.8 ± 0.15	4.2 ± 0.21	—
3.8–4.1	3.9–4.0	4.5–4.7	3.6–3.7	2.7–3.1	3.9–4.4	
—	5.2	7.5	5.5	4.1	6.1	76
	5.1–5.3	7.4–7.7	5.4–5.6	4.0–4.2	5.9–6.2	75–78
—	5.0	7.2	5.4	4.0	5.9	74
	5.0–5.1	7.2–7.3	5.4–5.5	3.0–4.0	5.7–6.1	72–76
—	6.4	9.2	6.6	5.2	7.7	89
	6.3–6.5	9.1–9.3	6.5–6.6	5.2–5.3	7.5–7.9	85–93

occurred within current park boundaries. Measurements are given in Table 6.

Specimens Examined—Total 1. Pasacao (1 usnm).

Hipposideros diadema (E. Geoffroy, 1813)

The diadem roundleaf bat is widespread in Indo-Australia (Koopman, 1984, 1989, 1993); it is found throughout the Philippines except in the Batanes/Babuyan region (Heaney et al., 1998). It appears to be most common in lowland areas, in both heavily disturbed and old-growth forest (Ingle, 1992; Lepiten, 1995; Rickart et al., 1993). We netted three adult females in disturbed lowland forest at 475 m (Site 1). Two pregnant females, weighing 31 and 50 g, each had a single embryo (CRL = 6 and 30 mm, respectively).

Specimens Examined—Total 3. Site 1 (3 usnm).

Hipposideros obscurus (Peters, 1861)

The Philippine forest roundleaf bat is a poorly known endemic species previously recorded from Greater Luzon, Greater Mindanao, and Greater Negros-Panay (Heaney et al., 1991, 1998; Rickart et al., 1993). Rickart et al. (1993) reported it from disturbed lowland forest at 600 m and old-growth mossy forest at 740 m on Maripipi, and Heaney et al. (1991) captured several in old-growth lowland forest at 250 m elevation on Catanduanes Island, one of which was roosting in a hollow log. Ingle (1992) found them in lightly disturbed lowland forest at 200–500 m elevation on Mount Makiling, Laguna Province. Lepiten (1995) found them in heavily disturbed lowland forest at 550 m elevation on Siquijor. We captured a single adult male (10 g) in disturbed forest at 475 m (Site 1; Fig. 16, Table 7).

Cranial measurements of the Mount Isarog specimen (Table 6) are similar to those of bats from Catanduanes (Heaney et al., 1991) and are slightly larger than those of a specimen from Dinagat (Heaney & Rabor, 1982) and a series from Maripipi (Rickart et al., 1993), indicating that significant geographic variation may occur in this species.

Specimens Examined—Total 1. Site 1 (1 usnm).

Hipposideros pygmaeus (Waterhouse, 1843)

The Philippine pygmy roundleaf bat is a poorly known endemic; it has been reported from Greater Luzon, Greater Mindanao, and Greater Negros-Panay (Heaney et al., 1998). We did not capture this species on Mount Isarog, but three adult male and two adult female specimens (Table 6) were

TABLE 6. *Extended.*

Species	Tail length	Hind foot	Ear	Forearm	Weight (g)
Emballonura alecto	9	6	13	47	5
	10	8	15	48	8
Megaderma spasma	0	20 ± 0.6	38 ± 1.5	58 ± 1.5	22.0 ± 0.82
	—	18–20	36–39	57–60	21–23
	0	19	40	59	25.0
	—	18–20	38–41	58–60	24.5–25.5
Hipposideros bicolor[a]	31	8	20	42	
Hipposideros diadema	47	18	29	81	39.7
	45–50	17–19	28–30	78–83	31–50
Hipposideros obscurus	20	12	18	44	10
Hipposideros pygmaeus	—	—	—	—	—
Rhinolophus arcuatus-1	21	11	23	46	8.5
	20–23	10–12	22–24	45–48	8–9
	21	11	21	44	12.5
	20–22	11	21	44-45	8–17
Rhinolophus inops	26	13	27	55	17
	25–27	13	26–27	55	15–18

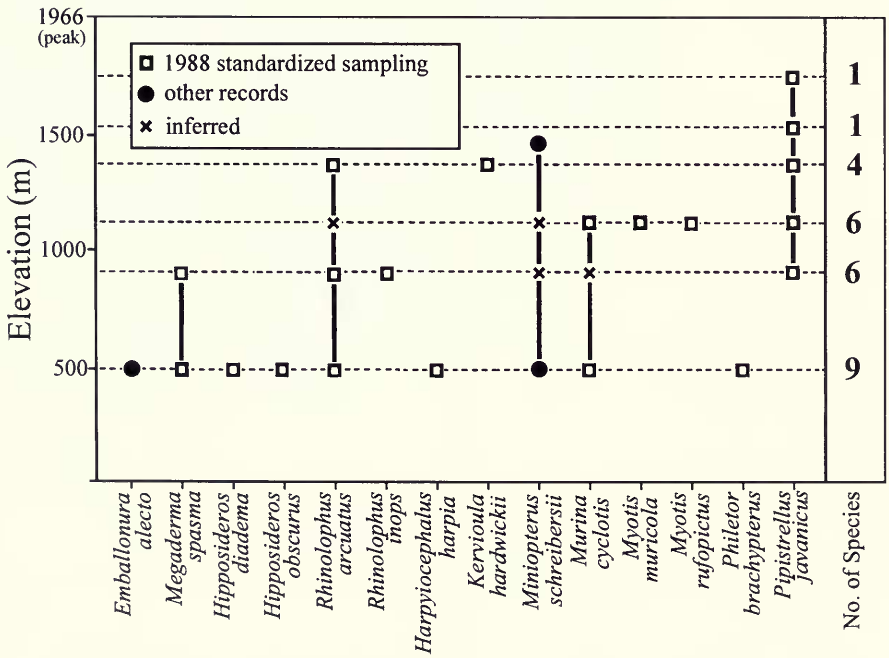

FIG. 16. Elevational distribution of insectivorous bats on Mount Isarog. Numbers in the right column indicate the number of species known to be present at a given elevation and those inferred to be present because they were taken both above and below in the 1988 transect study. Dotted lines indicate the elevation of intensive sampling sites.

TABLE 7. Abundance and elevational distribution of insectivorous bats on Mt. Isarog.

Species	Site and elevation (m) 1 475	2 900	3 1125	4 1350	5 1550	6 1750
Megaderma spasma	2	1	0	0	0	0
Hipposideros diadema	3	0	0	0	0	0
Hipposideros obscurus	1	0	0	0	0	0
Rhinolophus arcuatus-l	1	2	0	1	0	0
Rhinolophus inops	0	3	0	0	0	0
Kerivoula hardwickii	0	0	0	1	0	0
Harpiocephalus harpia	1	0	0	0	0	0
Murina cyclotis	2	0	1	0	0	0
Myotis muricola	0	0	2	0	0	0
Myotis rufopictus	0	0	1	0	0	0
Philetor brachypterus	1	0	0	0	0	0
Pipistrellus javanicus	0	2	3	31	18	3
Total species	7	4	4	3	1	1
Total bats	11	8	7	33	18	3
Total net-nights	75	54	56	63	66	26
Bats/net-night	0.15	0.15	0.12	0.52	0.27	0.12
Species/net-night	0.09	0.07	0.07	0.05	0.02	0.04

collected on an unknown date near Pasacao, where *H. bicolor* also was taken (see previous account); it should be sought in the area. All known records of this seemingly rare species are associated with caves in or near forest. Measurements are given in Table 6.

SPECIMENS EXAMINED—Total 1. Pasacao (5 USNM).

Rhinolophus arcuatus Peters, 1871

As currently defined, this species occurs from Sumatra to New Guinea (Koopman, 1989, 1993), probably including the entire Philippines. However, at least two species are currently suspected to be included under this specific epithet in the Philippines: a slightly smaller species, designated "*R. arcuatus*-s," associated with lowland caves, and a slightly larger species, "*R. arcuatus*-l," associated with upland old-growth forest (Heaney et al., 1991, 1998; Ingle & Heaney, 1992).

We netted three males and two females on Mount Isarog, in secondary lowland forest at 475 m, disturbed lowland forest at 900 m, and upper montane forest at 1350 m (Sites 1, 2, and 4; Fig. 16), all in March 1988. One of the males was captured while it foraged on fireflies (Lampyridae) over a partly cleared ridgetop adjacent to old-growth dipterocarp forest. Their habitat preference and cranial and external measurements suggest their close affinity to the *R. arcuatus*-l morphotype. One adult female (17 g) had a single embryo (CRL = 6 mm), and the other was nulliparous (8.5 g). Two of the males (8 and 8.5 g) had abdominal testes.

Cranial measurements (Table 6) are slightly smaller than those of specimens from Catanduanes and Negros (Heaney et al., 1991; Ingle & Heaney, 1992; specimens in USNM).

SPECIMENS EXAMINED—Total 5. Site 1 (1 USNM); Site 2 (2 USNM); Site 4 (2 USNM).

Rhinolophus inops Andersen, 1905

The Philippine forest horseshoe bat is a poorly known endemic reported previously from Greater Luzon, Greater Mindanao, Mindoro, and Greater Negros-Panay (Heaney et al., 1991, 1998; Rickart et al., 1993: specimens in USNM). On Biliran and Leyte, it was the most common microchiropteran encountered at most sites in old-growth lowland, montane, and mossy forest (Rickart et al., 1993). Heaney et al. (1991) encountered many in a cave in heavily disturbed lowland forest at 80 m elevation on Catanduanes. On Mount Isarog it was less common; we captured only three adult males (15–18 g) in a ridgetop clearing in old-growth dipterocarp forest at 900 m (Site 2).

Cranial measurements (Table 6) are larger than those of the series from Catanduanes, Luzon, and Negros (Heaney et al., 1991; specimens in USNM).

SPECIMENS EXAMINED—Total 3. Site 2 (3 USNM).

TABLE 8. Mean (± SD) and range of selected cranial and external measurements of adult microbats (Vespertilionidae) from Mt. Isarog, southern Luzon, Philippines. Sample size smaller than N is indicated by the number enclosed in parentheses after the range. Measurements taken from sample size of 2 are given as averages and their ranges. All measurements except weight are in millimeters.

Species	Sex	N	Condylo-incisive length	Zygomatic breadth	Inter-orbital width	Condylo-canine length	Mastoid breadth
Harpiocephalus harpia	M	1	20.3	13.6	5.5	19.7	11.3
Kerivoula hardwickii	F	1	12.8	8.1	2.9	12.1	7.3
Miniopterus schreibersi	M	1	14.6	8.4	3.8	13.5	8.3
Murina cyclotis	F	2	17.4	11.1	4.8	16.6	9.2
			17.4–17.5	11.1	4.7–4.9	16.5–16.8	9.2–9.3
Myotis muricola	M	1	13.8	(9.4)	3.6	12.8	7.7
	F	1	14.0	9.3	3.5	12.9	7.6
Myotis rufopictus	F	1	17.0	11.8	4.5	15.9	9.1
Philetor brachypterus	M	1	—	—	—	—	—
Pipistrellus javanicus	M	10	13.4 ± 0.21	9.3 ± 0.21	3.8 ± 0.13	12.7 ± 0.23	8.1 ± 0.19
			13.2–13.9	9.1–9.8	3.6–4.0	12.4–13.2	7.8–8.3
	F	6	13.5 ± 0.19	9.3 ± 0.32	3.7 ± 0.14	12.7 ± 0.15	8.0 ± 0.19
			13.2–13.7	8.8–9.6	3.5–3.9	12.5–12.9	7.8–8.3

Family Vespertilionidae—Common bats

Harpiocephalus harpia (Temminck, 1840)

The hairy-winged bat is widespread in Asia, from India to the Moluccas (Koopman, 1989, 1993); its occurrence in the Philippines was previously documented on Leyte, Negros, and Panay (Heaney et al., 1993, 1998; Utzurrum, unpubl. data). One adult male (15 g) was captured in disturbed lowland dipterocarp forest at 475 m (Site 1). This was the first record of this species on Luzon and was referred to by Ingle and Heaney (1992) and Heaney et al. (1998). An additional record from Luzon was reported by Ingle (1993). Measurements are given in Table 8.

SPECIMENS EXAMINED—Total 1. Site 1 (1 USNM).

Kerivoula hardwickii (Horsfield, 1824)

The common woolly bat is widespread from India and southern China to the Lesser Sunda Islands (Koopman, 1989, 1993); in the Philippines it was previously recorded only on Greater Mindanao (Leyte, Mindanao, and Samar) and Palawan (Heaney et al., 1998; Rickart et al., 1993). In March 1988, we captured a single specimen of this species, a pregnant female (5 g) with a single embryo (CRL = 8 mm), in upper montane forest at 1350 m (Site 4; Table 7). Rickart et al. (1993) noted two specimens from old-growth lowland forest at 500 m and old-growth ridgetop mossy forest at 950 m on Leyte. Cranial measurements are given in Table 8.

SPECIMENS EXAMINED—Total 1. Site 4 (1 USNM).

Miniopterus schreibersi (Kuhl, 1819)

The common bent-wing bat occurs from Africa through Europe to the Solomon Islands and Australia (Koopman, 1984, 1989, 1993); it is found throughout the Philippines, where it is common and usually dependent on caves (Heaney et al., 1991, 1998; Rickart et al., 1993). In December 1989, two adult males were captured with an insect net while they were apparently pursuing insects attracted by the bright fluorescent lights of a building at 1450 m (Site 16; Fig. 16).

In a shallow tunnel along the Tabuan River, 475 m elevation (Site 11), we collected a decomposing specimen of undetermined sex on the tunnel floor in 1989. There were ca. 25 *E. alecto* roosting in this tunnel, but we were not able to collect other specimens of *M. schreibersi*. Balete returned to the same site in April 1994 and found that it supported a colony of ca. 50 bats, but only *E. alecto* was seen. Measurements are given in Table 8.

SPECIMENS EXAMINED—Total 3. Site 11 (1 FMNH); Site 16 (2 UPLB).

Murina cyclotis Dobson, 1872

The round-eared tube-nosed bat is widespread in southern Asia (Koopman, 1989, 1993) but was

TABLE 8. *Extended.*

Rostral length	Orbital length	C1 to last M	Molariform tooth row	Palatal breadth at last M	Palatal length	Total length
5.5	7.6	7.0	5.0	4.0	9.7	113
3.9	3.5	5.6	3.5	2.6	6.8	78
4.3	4.8	6.0	4.3	3.7	6.3	
4.6	6.4	6.2	5.2	3.6	8.1	99
4.5–4.7	6.4	6.2–6.3	5.1–5.2	3.4–3.7	8.1	98–101
4.2	4.8	5.4	4.1	3.1	6.3	92
4.0	4.9	5.6	4.0	3.0	6.1	83
4.8	6.5	7.1	5.4	3.8	8.4	115
—	—	—	—	—	—	102
3.3 ± 0.13	5.2 ± 0.21	5.0 ± 0.16	3.8 ± 0.14	3.3 ± 0.16	4.8 ± 0.31	86 ± 2.6
3.2–3.6	4.9–5.6	4.9–5.3	3.6–4.1	3.1–3.6	4.5–5.5	81–91 (20)
3.5 ± 0.15	5.1 ± 0.18	5.0 ± 0.16	3.9 ± 0.08	3.2 ± 0.11	5.0 ± 0.17	87 ± 2.7
3.3–3.7	4.8–5.3	4.8–5.2 (6)	3.8–4.0 (6)	3.0–3.3 (6)	4.9–5.3	83–91

known previously in the Philippines from single specimens from Biliran, Camiguin, Catanduanes, Luzon, Mindanao, Sibuyan, and Siquijor (Heaney et al., 1991, 1998; Lepiten, 1997; Rickart et al., 1993); two additional specimens from Zambales Province were taken in lightly disturbed montane forest at 1100 m and 1500 m (Ruedas et al., 1994). We netted two females in disturbed lowland dipterocarp forest at 475 m (Site 1), and another female was taken in old-growth montane forest at 1125 m (Site 3; Fig. 16). The specimen from Biliran was netted in partially logged lowland forest at 700 m (Rickart et al., 1993); the one from Catanduanes was netted in disturbed lowland forest along a river at 200 m (Heaney et al., 1991), and one from Siquijor was netted in heavily disturbed lowland forest at 550 m (Lepiten, 1995). Two females (11 and 13 g) netted in April 1988 were pregnant with two embryos each (CRL = 15–16 mm). A lactating multiparous female (11 g) caught in May 1988 was not pregnant. Cranial measurements are given in Table 8.

SPECIMENS EXAMINED—Total 3. Site 1 (2 USNM); Site 3 (1 USNM).

Myotis muricola (Gray, 1846)

The whiskered myotis, found from Afghanistan to New Guinea (Koopman, 1993), has been recorded throughout the Philippines (Heaney et al., 1998). On Leyte, specimens were netted in disturbed and old-growth lowland forest at 50 m and 500 m, respectively; at 50 m, 700 m, and 850 m in forest plantation, disturbed lowland forest, and old-growth montane forest, respectively, on Biliran; and near sea level in a village on Maripipi Island (Rickart et al., 1993). Ruedas et al. (1994) reported two at 1100 m and 20 at 1500 m in lightly disturbed montane forest in Zambales Province, and Ingle (1992) captured several in lightly disturbed forest at 200–500 m elevation on Mount Makiling, Laguna Province. On Mount Isarog, we captured two specimens in old-growth montane forest at 1125 m (Site 3), an adult male (6.7 g) and an adult female (8 g) with a single embryo (10 mm CRL). Measurements are given in Table 8.

SPECIMENS EXAMINED—Total 2. Site 3 (2 USNM).

Myotis rufopictus (Hodgson, 1835)

The orange-fingered myotis is a Philippine endemic known only from Luzon (Mudar & Allen, 1986; Taylor, 1934), Negros, Palawan (Allen, 1922), and Sibuyan (Heaney et al., 1998). In March 1988 we captured an adult nulliparous female (9.7 g) in lower montane forest at 1125 m (Site 3; Table 7). The specimen from northeastern Luzon was taken over a stream in old-growth lowland forest at 50 m (Mudar & Allen, 1986). Measurements are given in Table 8.

SPECIMENS EXAMINED—Total 1. Site 3 (1 USNM).

Philetor brachypterus (Temminck, 1840)

The short-winged brown bat occurs from Nepal to New Guinea (Koopman, 1993), with previous

TABLE 8. *Extended.*

Species	Tail length	Hind foot	Ear	Forearm	Weight (g)
Harpiocephalus harpia	47	12	17	48	15
Kerivoula hardwickii	38	9	14	33	5
Miniopterus schreibersi	—	—	—	—	—
Murina cyclotis	40	11	16	39	11
	38–42	10–12	16–17	39	11
Myotis muricola	35	11	14	35	6.7
	35	11	15	37	8
Myotis rufopictus	53	11	19	49	9.7
Philetor brachypterus	38	11	12	38	11.8
Pipistrellus javanicus	34 ± 1.5	9 ± 0.6	12 ± 0.2	34 ± 0.9	7.1 ± 0.55
	32–38 (20)	8–10 (20)	12–13 (20)	32–36 (20)	6.5–8 (19)
	35 ± 1.7	9 ± 0.5	12 ± 0.7	35.5 ± 0.79	7.0 ± 0.69
	33–38 (9)	9–10 (7)	11–13 (9)	34–36.5 (9)	6–8 (9)

Philippine records from Catanduanes, Leyte, Mindanao, and Negros (Heaney et al., 1998; Rickart et al., 1993). The Leyte specimen was netted at 500 m in old-growth lowland forest (Rickart et al., 1993). In March 1988 we captured an adult male (11.8 g) with scrotal testes (3.5 × 7 mm) along a roadside in mixed secondary lowland forest and agricultural land at 475 m (Site 1). Although these were the first records from Luzon, Ingle (1992) reported two additional specimens netted in lightly disturbed lowland forest at 200–500 m on Mount Makiling, Laguna Province, demonstrating their broader distribution on Luzon. Measurements are given in Table 8.

SPECIMENS EXAMINED—Total 1. Site 1 (1 USNM).

Pipistrellus javanicus (Gray, 1838)

The Javan pipistrelle is found from Korea to Java (Koopman, 1993) and occurs throughout the Philippines (Heaney et al., 1998). It was the most frequently netted microchiropteran on Mount Isarog. We captured 39 males and 18 females along the western transect in 1988 (Table 7). They were not captured in disturbed lowland forest at 475 m (Site 1), were uncommon in lowland and lower montane forest at 900 m (Site 2) and 1125 m (Site 3), were abundant in montane and transitional montane–mossy forest at 1350 m (Site 4) and 1550 m (Site 5), and were uncommon in mossy forest at 1750 m (Site 6; Fig. 16, Table 7). Ingle (1992) found them to be moderately common in lightly disturbed lowland forest at 200–500 m elevation on Mount Makiling, Laguna Province.

Of the 39 males captured, 15 were adults (7.0 ± 0.52 g, N = 14) with scrotal testes ranging from 1 × 2 mm to 3 × 4 mm. Eleven other males (6.6 + 0.38 g) had abdominal testes; two of these had testes sizes of 1 × 3 mm and 2 × 3 mm. None of the adult females (7.0 ± 0.69 g, N = 9) displayed detectable reproductive activity. In January 1994, two of three males netted at Site 18 had scrotal testes measuring 3 × 4 mm and 4 × 5 mm. The third had abdominal testes. Measurements are given in Table 8.

SPECIMENS EXAMINED—Total 60. Site 2 (2 USNM); Site 3 (3 USNM); Site 4 (31 USNM); Site 5 (18 USNM); Site 6 (3 USNM); Site 18 (3 FMNH).

Order Primates

Family Cercopithecidae—Monkeys

Macaca fascicularis (Raffles, 1821)

The long-tailed macaque occurs from Burma to Timor and is found throughout the Philippines (Fooden, 1991, 1995). In 1988, we saw or heard the calls of this species at all sampling sites except 1750 m (Site 6), but densities were quite low and the animals were very wary. During our study on the southern side of Mount Isarog from November 1989 to February 1990, we encountered only one individual, in secondary lowland forest at 700 m (Site 14).

According to local residents, monkeys were actively hunted within the park prior to and during our field studies. We obtained an adult in March 1988 that had been captured as a pet about 1 year before on the lower western slopes of Mount Isarog. Two male juveniles kept as pets were seen in barangay Del Rosario, at 300 m elevation (Site 8) on the south side of Mount Isarog. At the same locality, two lower mandibles of recently killed and eaten macaques, a subadult (judging from the presence of some milk teeth and unerupted permanent teeth) and an adult, were acquired from a local resident.

SPECIMENS EXAMINED—Total 3. Unknown elevation (2 FMNH, lower mandibles only; 1 USNM).

Order Rodentia

Family Muridae—Rats and mice

Apomys microdon Hollister, 1931

The small Luzon forest mouse (Fig. 17) is endemic to the Luzon region and currently is known only from Catanduanes Island, Mount Isarog, and the Sierra Madre of northern Luzon (Danielsen et al., 1994; Heaney et al., 1991; Musser & Heaney, 1992; Rickart et al., 1991). It is easily distinguished from the sympatric *A. musculus* by its larger size (total length 226–256 vs. 188–213 mm; basioccipital length 25.1–27.4 vs. 23.4–24.7 mm; Table 9).

During 1988, seven adult specimens of this medium-sized species (35.1 ± 3.7 g) were taken at elevations ranging from 475 to 1550 m in disturbed lowland forest, old-growth montane forest, and mossy forest (Rickart et al., 1991; Fig. 12). The study in 1993–1994 at Site 18 recorded no individuals of this species between 1650 and 1700 m (Balete, 1995). All specimens collected in 1988 were taken at night in traps baited with coconut and set on the ground in areas of heavy cover (0.07–0.33% trap success; Table 2 in Rickart et al., 1991). Stomach contents of three snap-trapped specimens included remains of larval and adult insects as well as seed fragments. The species is probably best described as an insectivore/omnivore.

All three specimens taken at Site 1 (475 m) were caught at the base of large ferns. One female (42 g) taken in early March was pregnant with three embryos (CRL = 21 mm), and one (33.5 g) caught in late April had two recent placental scars. Two adult males (24 and 35 g) taken in March and one adult male (34 g) trapped in April had testes ranging from 3 × 8 mm to 4 × 7 mm. Measurements are given in Table 9.

SPECIMENS EXAMINED—Total 7. Site 1 (3 USNM); Site 3 (1 USNM); Site 4 (1 USNM); Site 5 (2 USNM).

Apomys musculus Miller, 1911

The least Luzon forest mouse (Fig. 17) is known only from Dinagat, Luzon, and Mindoro islands (Heaney et al., 1998; Musser, 1982a). Specimens of this small mouse (21.2 ± 1.8 g) were trapped from 1125 to 1750 m in old-growth montane and mossy forest and were significantly more common in montane forest (Rickart et al., 1991; Fig. 12). Trap success ranged from 0.09% to 1.09% per trap-night with coconut bait and from 0.21% to 0.73% per trap-night with live earthworm bait; there was no significant difference in overall bait attractiveness ($\chi^2 = 0.008$, $P > 0.9$).

At Site 18, this was the most commonly trapped species, accounting for 62% of the total number of individuals captured. The mean density of *A. musculus* (8.8 individuals/ha) was the highest among rodents in the mossy forest, whereas its biomass (163.2 g/ha) was the second lowest (Table 10). Mean distance moved (MDM) between captures was 42 m (±42.3 m), and intersex difference in MDM was significant ($t = -0.583$, $P > 0.05$). Maximum distance traveled between captures ranged from 150 to 190 m among males and from 191 to 226 m among females. Individual home range size of 15 mice (9 males and 6 females) was estimated to be about 0.22 ha (range 0.01–0.56 ha), with home ranges of males (0.15 ha) averaging about half that of females (0.32 ha). Between 20% and 100% of the home range of any given individual overlapped with the home range of a conspecific (Balete, 1995; Balete & Heaney, 1997).

Stomach contents of four snap-trapped specimens included remains of insect larvae (Diptera, Coleoptera) and fragments of seeds. A captive individual readily accepted several types of fruit, young sedge leaves, coconut bait, peanuts, sweet potato, insect larvae, adult beetles, cicada, harvestmen, and raw meat. Earthworms, millipedes, adult ants, cockroaches, and a tree fern "fiddle head" were accepted when the animal was hungry, but the items listed first appeared to be preferred. The captive mouse rejected some seeds

TABLE 9. Mean (± SD) and range of selected cranial and external measurements of adult murid rodents (Muridae) from Mt. Isarog, southern Luzon, Philippines. Sample size smaller than N is indicated by the number enclosed in parentheses after the range. Measurements taken from sample sizes of 2 and 3 are given as averages and their ranges. All measurements except weight are in millimeters.

Species	Sex	N	Basioc-cipital length	Inter-orbital width	Zygomatic breadth	Mastoid breadth
Apomys microdon	M	3	26.0	4.6	13.8	12.0
			25.1–26.8 (2)	4.4–4.9 (2)	13.4–14.3 (2)	11.7–12.3 (2)
	F	4	26.3 ± 0.80	4.6 ± 0.10	14.3 ± 0.48	12.1 ± 0.28
			25.5–27.4	4.5–4.7	13.6–14.7	11.8–12.4
Apomys musculus	M	10	24.2 ± 0.33	4.3 ± 0.13	13.2 ± 0.22	11.2 ± 0.22
			23.7–24.7	4.1–4.5	12.9–13.6 (7)	11.0–11.5
	F	8	23.8 ± 0.34	4.2 ± 0.10	13.1 ± 0.16	11.2 ± 0.26
			23.4–24.4	4.1–4.4	12.8–13.3	10.8–11.5
Archboldomys luzonensis	M	5	25.6 ± 0.64	5.4 ± 0.14	13.3 ± 0.11	11.7 ± 0.08
			24.7–26.1	5.2–5.6	13.2–13.4	11.6–11.8
	F	2	25.2	5.6	13.4	11.8
			25.0–25.5	5.5–5.6	13.4–13.5	11.7–11.8
Batomys granti	M	4	40.6	5.7 ± 0.05	22.5 ± 0.53	15.6
			40.1–41.1 (3)	5.6–5.7	21.9–23.1	15.4–15.8 (3)
	F	2	39.2	6.0	20.5 (1)	15.2
			37.6–40.7	5.9–6.0	—	14.7–15.6
Chrotomys gonzalesi	M	2	—	7.7	21.4	17.1 (1)
				7.6–7.8	21.3–22.4	—
	F	3	38.0	7.5	20.0	16.3
			36.8–38.6	7.1–7.7	18.8–20.8	15.8–16.7

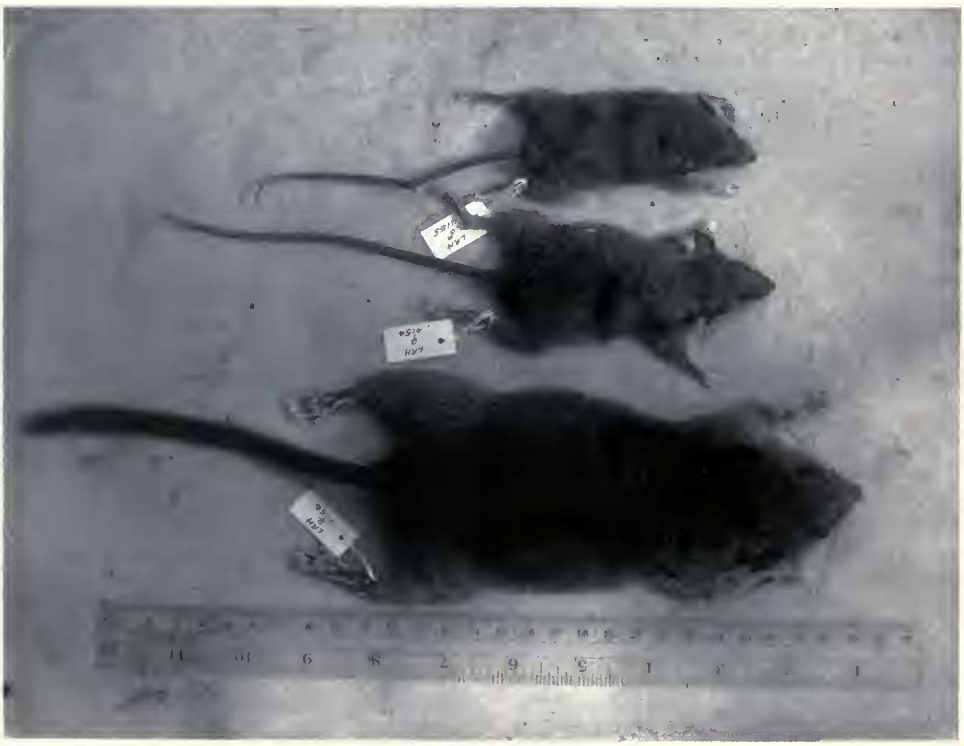

FIG. 17. Adult *Apomys microdon, Apomys musculus,* and *Batomys granti* (top to bottom), showing the relative size and proportions of these species. April 1988, Site 4, L. R. Heaney.

TABLE 9. *Extended.*

Nasal length	Anterior nasal width	Rostral depth	Rostral length	Orbital length	Maxillary molariform tooth row	Palatal breadth at P4	Diastema length
10.3	3.1	5.7	10.4	9.5	5.3	5.7	6.6
10.0–10.7	2.9–3.4	5.6–5.8	10.0–10.9	9.2–9.8	5.2–5.4	5.6–5.8	6.3–7.1
10.2 ± 0.45	3.2 ± 0.10	5.8 ± 0.13	10.7 ± 0.22	9.9 ± 0.14	5.3 ± 0.13	5.7 ± 0.17	7.0 ± 0.24
9.7–10.8	3.0–3.3	5.7–6.0	10.0–11.0	9.8–10.1	5.2–5.5	5.5–5.9	6.3–7.3
9.2 ± 0.42	2.8 ± 0.19	5.4 ± 0.14	9.2 ± 0.28	9.2 ± 0.19	4.8 ± 0.11	5.4 ± 0.12	6.4 ± 0.20
8.5–9.8	2.5–3.0	5.3–5.8	8.8–9.8	9.0–9.5	4.6–4.9	5.2–5.5	6.1–6.8
9.0 ± 0.35	2.6 ± 0.13	5.3 ± 0.11	9.0 ± 0.28	9.2 ± 0.16	4.7 ± 0.11	5.2 ± 0.13	6.3 ± 0.18
8.3–9.4	2.4–2.8	5.1–5.4	8.4–9.3	8.9–9.4	4.5–4.8	5.0–5.4	6.0–6.8
9.6 ± 0.32	2.9 ± 0.08	5.1 ± 0.19	10.6 ± 0.42	9.0 ± 0.21	4.6 ± 0.15	5.8 ± 0.10	6.8 ± 0.25
9.3–9.4	2.8–3.0	4.9–5.3	10.1–11.1	8.8–9.3	4.4–4.8	5.7–5.9	6.5–7.1
9.6	3.1	5.1	10.5	8.9	4.7	5.8	6.9
9.2–9.9	3.1	5.1	10.3–10.7	8.8–9.0	4.7	5.8–5.9	6.7–7.1
16.4 ± 0.76	5.0 ± 0.47	9.5 ± 0.14	17.7 ± 1.11	13.9 ± 0.53	8.4 ± 0.42	8.0 ± 0.40	11.4 ± 0.66
15.7–17.4	4.4–5.4	9.4–9.7	16.2–18.8	13.5–14.7	7.9–8.8	7.6–8.5	10.8–12.3
15.8 (1)	5.0 (1)	9.4	16.5 (1)	13.4	8.4	7.9	11.0
—	—	8.7–10.2	—	13.0–13.7	8.3–8.4	7.7–8.1	10.0–11.9
12.8 (1)	3.8 (1)	7.7 (1)	14.4 (1)	13.8	6.2	7.4	15.4 (1)
—	—	—	—	13.4–14.2	6.1–6.3	7.4–7.5	—
12.2	3.7	7.2	13.1	12.8	6.0	6.9	13.9
12.1–12.3	3.4–3.9	6.9–7.6	12.7–13.3	12.1–13.4	5.9–6.2	6.7–7.0	13.2–14.3

and seedlings, some kinds of fruit, the root of a ginger plant, a hard-shelled larva, tender young leaves, a mushroom, moss, large ants, rove beetles, caterpillars, and a longhorn beetle. Remains of possible food items collected along runways where this species was captured at Site 18 (Balete, 1995) included the shell of an unidentified land snail, acorns of *Lithocarpus* sp. (Fagaceae), and seeds of *Languas scabra* (Zingiberaceae). A fruit of *Schima* sp. (Theaceae) that apparently had been gnawed by an *Apomys*, judging from the fine teeth marks, was found in a tree fork ca. 5 m above ground at the same site. All of these plant species are common in forest at Sites 5, 6, and 18 (Table 1). This species is best described as an omnivore.

All specimens recorded in 1988 (during a relatively dry period) were taken at night, primarily along surface runways in areas of moderate to heavy cover. At Site 18, 11 individuals (23%) were captured between midday and 16:00 (Balete, 1995) during a season of generally heavy rain. Many individuals were caught in tree root complexes, at openings to tunnels along the sides of steep ravines, and beside or beneath fallen logs. Two animals were taken in traps set on top of fallen logs (one of which was more than 1 m above the ground), indicating that they are somewhat scansorial. A *Crocidura grayi* was captured in a trap (in a runway beneath a small log) that had caught an *A. musculus* the previous day. Scats of viverrids collected in the mossy forest at Site 18, 1550–1600 m, contained remains of this species (Table 12).

Two adult females (22 and 23 g) caught in late April 1988 each had two embryos (CRL = 9 and 20 mm). Litter size was 2.0, based on counts of embryos and uterine scars in four females. Adult and young adult males taken in March and April were reproductively active. Seven adults (20.7 ± 1.82 g) and two young adults (18 and 20 g) had scrotal testes ranging in size from 4 × 6 mm to 5 × 11 mm. Two immature animals caught in late March and late April weighed 10 and 14.5 g. At Site 18, males and females began to exhibit signs of reproductive activity (scrotal testes, perforate vaginas, enlarged mammae) in March (Balete, 1995). None of the females, however, was pregnant when the study was concluded in May 1994.

Two males first captured and marked in January 1994 as subadults (15 and 15.5 g, with dark, soft fur and abdominal testes) were recaptured in March with descended testes and weighing 17.5 and 18.5 g. In addition, a female (15 g) first captured in February with an imperforate vagina was recaptured in mid-March weighing 15.5 g and with a perforate vagina. These are indications that

TABLE 9. *Extended.*

Species	Total length	Tail length	Hind foot	Ear	Weight (g)
Apomys microdon	238	134	27	17	31
	226–256	125–145	25–28	17–18	24–35
	238 ± 12.3	131 ± 3.4	27 ± 1.0	17 ± 0.5	35.4 ± 4.71
	227–254	128–136	26–28	16–17	31–42
Apomys musculus	205 ± 8.8	112 ± 4.7	24 ± 0.4	16 ± 0.7	20.4 ± 1.73
	188–211 (8)	102–118 (9)	23–24 (11)	15–17 (11)	18–23 (11)
	209 ± 4.9	116 ± 3.4	24 ± 0.7	15 ± 0.7	21.8 ± 1.70
	200–213 (7)	112–121 (9)	23–25 (9)	15–17 (9)	19–24 (9)
Archboldomys luzonensis	178 ± 8.0	72 ± 6.7	28 ± 0.9	16.8 ± 0.65	35.3 ± 3.21
	167–190 (7)	60–80 (8)	26–29 (8)	16–18 (8)	31–41 (9)
	176 ± 4.3	72 ± 3.9	27 ± 1.1	17 ± 1.1	36.9 ± 6.80
	170–180 (4)	67–76 (5)	26–29 (5)	15–18 (5)	28.5–46.5
Batomys granti	340	144	37 ± 1.5	21.3	173 ± 8.8
	331–355 (3)	140–149 (3)	35–38 (5)	21–22 (3)	160–200 (5)
	327 ± 16.4	145 ± 16.1	37 ± 1.5	20 ± 0.5	158 ± 16.6
	315–356 (5)	128–171 (5)	35–39 (5)	20–21 (4)	135–175 (4)
Chrotomys gonzalesi	272 ± 25.5	99 ± 8.2	37 ± 1.9	22 ± 1.1	146 ± 37.9
	232–293 (5)	87–105 (5)	34–39 (5)	20–23 (5)	98–190 (5)
	250 ± 14.2	91 ± 6.3	36 ± 1.0	21 ± 1.0	106 ± 29.7
	230–260 (4)	83–97 (4)	34–36 (4)	20–22 (4)	70–142 (4)

individuals of this species becomes reproductively active within their first year as they achieve adult weight. The mean weight of all animals captured and released in 1993–1994 increased steadily from 17.4 g (±1.97, N = 10) in December 1993 to 18.7 g (±1.41, N = 13) in April 1994 (Fig. 18) as the population shifted from an equal mixture of adults and subadults (in December) to nearly all adults in April (Fig. 19). This shift was accompanied by a shift from virtually no reproductive activity in December to increasing evidence of reproductive capacity (though no pregnancies) in April (Fig. 20).

TABLE 10. Mean density and biomass (± SD) of nonvolant small mammals in mossy forest on Mt. Isarog. From Balete and Heaney, 1998.

Species	Density (individuals/ha)	Biomass (g/ha)
Apomys musculus	8.8 ± 0.66	163.2 ± 21.20
Archboldomys luzonensis	4.5 ± 1.63	138.5 ± 50.04
Batomys granti	3.0 ± 0.67	591.5 ± 116.49
Rattus everetti	1.2 ± 0.05	333.3 ± 61.37
Rhynchomys isarogensis	2.6 ± 1.05	328.4 ± 113.36
All species	20.1	1554.9

Cranial and external measurements are given in Table 9. Specimens of this species from Mount Isarog have a standard karyotype of 2n = 42, FN = 52, and exhibit chromosomal similarities to both *Chrotomys* and *Rhynchomys* (Rickart & Musser, 1993).

SPECIMENS EXAMINED—Total 36. Site 3 (3 USNM); Site 4 (17 USNM); Site 5 (3 USNM); Site 6 (1 USNM); Site 18 (8 FMNH); Curry (4 FMNH).

Archboldomys luzonensis Musser, 1982

The Mount Isarog shrew-mouse (Fig. 21) is perhaps the most distinctive element of the mountain's mammal fauna. This genus and species was described based on a single specimen from 2400 ft. elevation (= ca. 750 m) on Mount Isarog captured by D. S. Rabor's field crew in 1961 (Musser, 1982b). Heaney et al. (1998) listed the species as vulnerable because of its highly limited distribution. A second species of *Archboldomys* from northern Luzon was described recently (Rickart et al., 1998).

In 1988 we captured eight specimens of this small mouse (35.4 ± 5.4 g) in old-growth montane forest at 1350 m and in old-growth mossy forest at 1750 m elevation (Fig. 12; Table 1 in

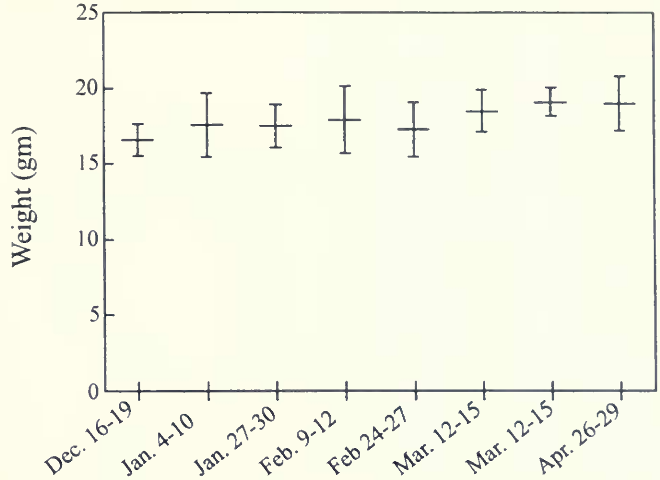

FIG. 18. Weight of all *Apomys musculus* livetrapped in mossy forest on Mount Isarog from December 1993 to April 1994, showing average progressive weight gain (from Balete, 1995).

Rickart et al., 1991). Six more specimens were captured in mossy forest at 1700–1800 m elevation at Site 17 in 1992. Balete (1995) estimated the density of this species at Site 18 to be 4.5 individuals/ha (±1.63), second only to *Apomys musculus* (Table 10), but its biomass, 138 g/ha (±50.0 g/ha), was the lowest among the nonvolant small mammals in mossy forest (Table 10). We consider the species to be moderately common in mossy forest, rare in montane forest, and absent elsewhere.

All individuals captured in 1988 were taken in traps baited with coconut (0.22–0.47% trap success). However, the positions of snap-trapped animals suggested that they were not attracted to the bait but rather had accidentally triggered traps set in runways; three animals taken alive were caught by the tail or a hind leg. All six specimens cap-

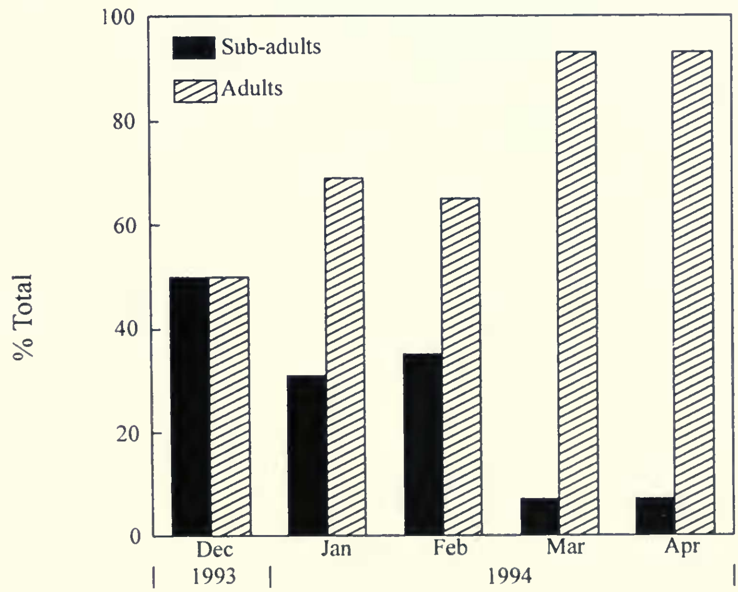

FIG. 19. Age structure of *Apomys musculus* in mossy forest on Mount Isarog from December 1993 to April 1994 (from Balete, 1995).

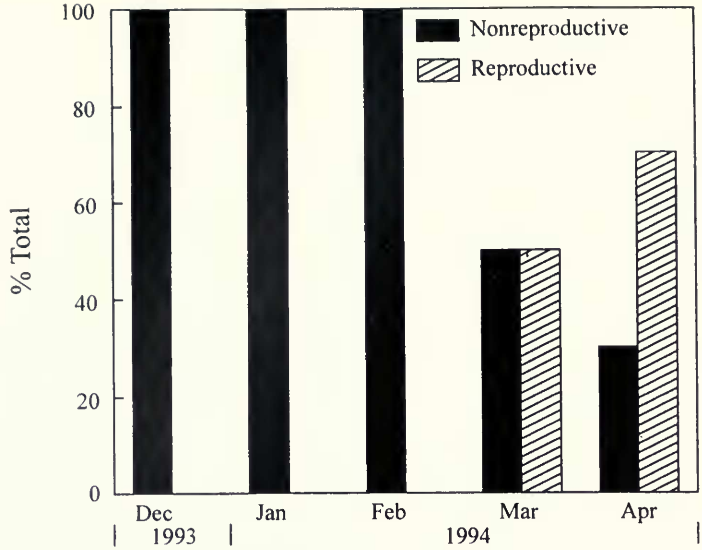

FIG. 20. Reproductive condition of *Apomys musculus* in mossy forest on Mount Isarog from December 1993 to April 1994 (from Balete, 1995).

FIG. 21. Adult *Archboldomys luzonensis*. March 1988, Site 4, E. A. Rickart.

tured in 1992 were taken in snap traps baited with earthworms (6.00% trap success). Data on movements were meager; one female was recaptured within 2 days of its initial capture and 92 m from the initial point of capture (Balete, 1995; Balete & Heaney, 1997).

Stomachs of four snap-trapped individuals included remains of larval insects (Diptera), adult insects (Diptera, Orthoptera, Coleoptera), terrestrial amphipods, and earthworms, all of which were abundant in the area of Sites 5, 6, and 18 (Tables 3 and 4). None contained identifiable plant material. One captive individual readily accepted several kinds of earthworms, live adult flies, and an adult weevil. Fresh rat flesh and dried meat were accepted less avidly, and all types of plant material were rejected. This species is best described as a generalist insectivore.

The Mount Isarog shrew-mouse is primarily if not exclusively diurnal. Seven of the eight animals captured in 1988 (87.5%) were trapped during daylight hours, and one was taken near dawn. In the 1993–1994 study, Balete (1995) recorded two individuals foraging in the mossy forest during daylight. All specimens were caught on the ground in areas of heavy cover. Most were taken in traps set along well-defined runways, either under logs or root tangles or beneath mixed masses of vines, small live plants, and dead vegetation. The chunky body, short limbs and tail, small ears, and short, dense pelage indicate that *A. luzonensis* probably is semifossorial.

Scats of viverrid carnivores collected in the mossy forest at other sites did not yield evidence of predation on this species (Balete, 1995; Table 12).

Five adult females were trapped in late March and late April, three of which had two pairs of enlarged mammae. Two pregnant females (37 and 47.5 g) each had a single embryo (CRL = 14 and 17 mm). Two adult males (33 and 35 g) taken during the same period had scrotal testes of 3 × 6 mm and 6 × 11 mm. A female collected in January 1994 also had enlarged mammae; its reproductive tract showed signs of swelling (Balete, 1995).

Cranial and external measurements appear in Table 9. *Archboldomys* has a karyotype of 2n = 26, FN = 43 that is distinctive; both sexes possess heteromorphic sex chromosomes (Rickart & Musser, 1993; Rickart et al., 1998).

Specimens Examined—Total 17. Site 4 (3 usnm); Site 6 (5 usnm), holotype (1 fmnh); Site 17 (3 fmnh, 3 pnm); Site 18 (2 fmnh).

Batomys granti Thomas, 1895

The Luzon hairy-tailed rat (Fig. 17) previously was known only from Mount Data in the Central Cordillera of northern Luzon (Musser & Heaney, 1992; Musser et al., 1998). In 1988, we trapped 13 individuals of this medium-sized rat (177.8 ± 20.3 g) in upper montane and mossy forest from 1350 to 1750 m (Fig. 12), and Balete caught a single specimen in mossy forest at 1800 m in 1990. They were significantly more common in mossy forest than in other habitats (Table 1 in Rickart et al., 1991). Trap success in 1988 ranged from 0.07% to 0.47% per trap-night with coconut bait and from 0% to 0.24% per trap-night with earthworm bait, with no significant difference in overall bait attractiveness ($\chi^2 = 0.203$; $P > 0.5$). Many animals apparently were caught accidentally by traps set in their well-defined runways rather than because of bait attraction. In 1993–1994, live-trapped *B. granti* were taken in significantly higher frequency with coconut bait (Balete, 1995). The one specimen from the southern transect (Site 17) was taken in a trap baited with dried squid, but it too may have been an accidental capture.

Mean density of *B. granti* estimated in the mark-and-recapture study in 1993–1994 was 3.0 individuals/ha (±0.67), third behind *Apomys musculus* and *Archboldomys luzonensis*. In contrast, its biomass of 591.5 g/ha (±116.40) was the highest of all rodents (Table 10). Data on the movement of this species were very limited; one female trapped five times on three successive days had a mean distance moved of 11 m (range 5–14 m), and another female captured eight times in 3 months had a mean distance moved of 44 m (±23.0 m, range 14–85 m). The latter female was estimated to have a home range of 0.11 ha (Balete, 1995; Balete & Heaney, 1997).

The stomachs of snap-trapped specimens all contained finely masticated vegetable material (seeds and leaves) with no trace of chitin or other animal matter. A captive animal avidly accepted small dicot seeds that were sprouting on the forest floor at the upper elevations at the time of our study in 1988. Only the cotyledons were eaten; the sprouts were removed and rejected. Several other potential food items, including earthworms, insects, and various plant matter, also were rejected. Clearly, this species is a granivore/frugivore.

All specimens were caught at night. Most were trapped in runways along the sides of ravines or on the ground in steep terrain in areas of moderate to heavy cover, sometimes in places where they had climbed through lattices of roots, branches, and moss that extended well above solid ground. In contrast to the two other predominantly nocturnal species (*Apomys musculus* and *Rattus everetti*), the scats of viverrids did not reveal evidence of predation on this species (Table 12).

There was no evidence of reproductive activity during either field period. Nulliparous females (128 ± 32.8 g) with small nipples were taken in late March and late April. Two females (175 and 220 g) taken in late April had old placental scars (three and four) but were not lactating. Two adult males (160 and 175 g) caught in late April had abdominal, inactive testes of 7 × 13 mm and 12 × 22 mm, and another two males (176 and 200 g) had scrotal testes, one of which had a testes size of 7 × 12 mm. None of the individuals marked and recaptured at Site 18 from December 1993 until May 1994 showed signs of reproductive activity (Balete, 1995).

In the closely related *B. salomonseni*, Rickart et al. (1993) encountered no evidence of breeding during the dry season (March and April) on Leyte or Biliran, although they also encountered large juveniles during this season. These data suggest that most reproduction in these two species takes place during the early rainy season, from June to August.

Measurements are provided in Table 9. Specimens from Mount Isarog have a karyotype of 2n = 52, FN = 52, consisting entirely of telocentric chromosomes. The standard karyotype is indistinguishable from that of *Batomys salomonseni* from the Mindanao Faunal Region (Rickart & Musser, 1993; Musser et al., 1998).

Specimens Examined—Total 15. Site 4 (1 usnm); Site 5 (6 usnm); Site 6 (6 usnm); Site 17 (1 fmnh); Site 18 (1 fmnh).

Bullimus luzonicus (Thomas, 1895)

The large Luzon forest rat is a Luzon endemic (Heaney et al., 1998; Musser & Heaney, 1992). The only record from southern Luzon is a series at the Florida Museum of Natural History from the vicinity of Caramoan (13°47′N, 123°51′E), ca. 50 km east of Mount Isarog. These specimens were taken in 1982–1983 from an area of mixed old-growth and disturbed lowland dipterocarp forest with abundant bamboo, below 300 m elevation in a region dominated by karst (Auffenberg, 1988; Wilkins, pers. comm.). If the species occurs on Mount Isarog, it is probably confined to areas of remnant forest below 900 m elevation.

Specimens Examined—Total 6. Near Caramoan (6 fsm).

Chrotomys gonzalesi Rickart and Heaney, 1991

The Isarog striped shrew-rat (Fig. 22) is a strikingly colored, medium-sized (140.2 ± 36.3 g) animal known only from Mount Isarog. It is represented by eight specimens trapped in 1988 (Rickart & Heaney, 1991; Rickart et al., 1991) in upper montane forest at 1350 m elevation and in mossy forest at 1750 m elevation (Sites 4 and 6; Fig. 12) and two taken in 1992 in mossy forest at 1800 m (Site 17). Three individuals were livetrapped and tagged in the mossy forest at 1550 m (N = 1) and 1650 m (N = 2) within a period of 5 months at Site 18 in 1993–1994. The mark–recapture study at Site 18 obtained so few data on this species that density, biomass, and home range size could not be estimated (Balete & Heaney, 1997). Scats of viverrids collected at 1150–1600 m did not contain remains of this species (Table 12).

In 1988, six animals were caught in traps baited with earthworms (three at each site, 0.66% and 0.88% trap success), and two were caught with coconut bait at 1350 m (0.15% success); the greater success with earthworm bait is significant ($\chi^2 = 8.232$; $P < 0.005$; Rickart et al., 1991). All three rats captured and released in 1993–1994 were taken with earthworm bait. Stomachs of five snap-trapped animals contained remains of earthworms, terrestrial amphipods, insect larvae (Coleoptera, Diptera), adult insects (Orthoptera, Diptera), and spiders, all of which are abundant in the area of Sites 5, 6, and 18 (Tables 2 and 3). No traces of plant material were noted. This species is best described as a vermivore/insectivore.

Individuals of this species were active both day and night; of eight specimens captured in 1988, three (37.5%) were caught during daylight hours, another at dusk, and the rest at night. All specimens were taken in traps set on the ground surface in areas of heavy cover. Most individuals were caught in runways beside fallen logs or in subsurface openings among exposed tree roots. The basic morphology (stout body, short strong limbs, stout tail, and large forefeet with strong claws) indicates a semifossorial mode of life.

An adult female (111 g) trapped in late March 1988 had prominent teats and five placental scars (probably two sets), and another adult (100 g)

FIG. 22. Adult *Chrotomys gonzalesi.* 28 April 1988, Site 3, L. R. Heaney.

taken in late April was pregnant with two embryos (CRL = 5 mm). Two adult males (160 g and 190 g) in breeding condition were caught during both months. Both had scrotal testes of 12 × 25 mm and both had visibly convoluted epididymides. Two young adult males (115 g and 165 g) taken in March 1988 were likewise approaching breeding condition, both having scrotal testes (7 × 20 mm and 14 × 19 mm) and visibly convoluted epididymides.

Measurements are given in Table 9. Rickart and Heaney (1991) provided additional measurements as well as comparisons with other species of *Chrotomys* and *Celaenomys.* The standard karyotype (only female specimens were examined) is 2n = 44, FN = 52; this is indistinguishable from the standard karyotype of female *Rhynchomys* (Rickart & Musser, 1993).

SPECIMENS EXAMINED—Total 10. Site 4 (5 USNM including holotype); Site 6 (3 USNM); Site 17 (1 FMNH, 1 PNM).

Mus musculus Waterhouse, 1843

The house mouse is a widespread commensal species in Southeast Asia and is abundant in Philippine urban areas (Heaney et al., 1998). An adult male and female were hand-caught in an open field newly planted with maize at ca. 350 m (Site 8). Both were inside a dry, empty coconut with a small hole on one end that served as the entrance. The male (10.5 g) had scrotal testes, and the female (9.5 g) had enlarged mammae. Another subadult female was trapped in an agricultural field immediately adjacent to a house at 475 m (Site 1).

SPECIMENS EXAMINED—Total 3. Site 1 (1 USNM); Site 8 (2 UPLB).

Phloeomys cumingi Waterhouse, 1839

The *bugkun* (or southern Luzon giant cloud rat; Fig. 23) is endemic to Catanduanes, Marinduque, and the southern part of Luzon (Heaney et al., 1991; Musser & Heaney, 1992), perhaps as far north as the mountains east of Manila (Oliver et al., 1993a). Populations have declined significantly in recent decades because of intense hunting and habitat destruction (Heaney & Utzurrum, 1991; Oliver et al., 1993a), but they remain common in some areas (Heaney et al., 1991, 1998).

FIG. 23. Adult *Phloeomys cumingi.* 5 March 1988, Site 1, L. R. Heaney.

This is one of the largest murid rodents; adults may weigh more than 2 kg.

In 1988, 11 specimens were obtained from local hunters in the Mount Isarog region. All were captured at sites between 200 and 500 m elevation in areas of disturbed forest along the Yabo River, a small river that flows down the western flank of the mountain. These remnant forest patches were confined to steep slopes near the river and were surrounded by agricultural land. Two lactating females (each weighing 1.85 kg) with a single nursing young each (370 and 610 g) were obtained on 2 and 4 March, and a postlactating female (1.85 kg) with a juvenile male (1.1 kg) was brought to us on 9 March. An adult male (2.05 kg) was obtained on 6 March. Heaney et al. (1991) reported comparable weights for adult females (1.45–2.1 kg), nulliparous females (1.14–1.15 kg), nursing young (480 and 665 g), old adult males (1.74 and 1.95 kg), and a young adult male (1.45 kg) from Catanduanes.

The first female/young pair was found in a hollow space in a large strangler fig tree, the second in a standing live hollow tree that they entered through a hole ca. 4 m aboveground, and the third in a standing, hollow dead tree (dbh ca. 35 cm). The adult male was captured as the sole occupant of a hollow standing tree. All were located by a dog and were forced to leave the tree because of smoke from a fire built at the base of the tree.

In February 1994, a viverrid scat collected in old-growth forest, ca. 1150 m, contained foot bones of an adult of this species (Table 12). This is the first recorded case of predation on this species, although scavenging might have been involved. Seeds of *Elaeocarpus luzonicus* (Elaeocarpaceae) as well as fruits and flowers of climbing pandans (*Freycinetia* sp.) were also found in the scat, suggesting a predator with omnivorous feeding habits. Currently, there is no known record of *P. cumingi* at this elevation and in the forest type where the scat was found, but lowland secondary forest occurred no more than 1 km distant.

Most local hunters apparently pursue cloud rats only as a sideline to hunting other larger species; i.e., they will catch the rats when they encounter them but do not specifically go out to hunt them. The hunter who captured most of the 1988 specimens reported that he had taken about 50 of them in the previous year and considered them to be quite common, as did other local inhabitants. All informants stated that they encountered them only in lowland forest, from about 150 m (the lowest elevation of patches of degraded forest) to about 900 m (the upper limit of lowland dipterocarp forest). Informants said that cloud rats occur even in very small patches of degraded forest that exist as discontinuous chains of habitat along the steep banks of rivers. Cloud rats are said to spend most of their time in the forest or scrub but also some time in agricultural fields. They reportedly require large hollow logs or trees for nest sites and do not persist without such sites. They are said to be active only at night and to always spend the day in hollow trees or logs.

Local residents told us that cloud rats eat the young leaves of papaya and other trees (both domestic and wild), sometimes the leaves of sweet potato (locally called *camote*), and both the leaves and fruit of sayote (*Sacchium edule*, a ground-growing squash). In Del Rosario (Site 9), a local hunter told us that *P. cumingi* fed on the clustered flame-red flowers of rarang (*Erythrina subumbrans*), which start to bloom in the midst of abaca and coffee plantations during the dry season. In February 1990, one animal was shot on such a tree in bloom in a coffee plantation close to the farmers' houses.

Our informants said that the giant rats usually have one young per litter but occasionally have two and rarely three in a litter. They said that females give birth in late November and December and that they have seen females with dependent young in February and March, which is usually the beginning of the dry season. The young were described as being "quite large" at birth, about "the thickness of a man's wrist." The young stay with the females for "a long time," and it is common to capture a female with a nearly fully grown subadult. An adult male and adult female are occasionally captured in the same hollow tree, and sometimes the females have young with them at the time. All of these comments are consistent with those from informants on Catanduanes (Heaney et al., 1991).

Cranial measurements (Table 11) are slightly larger than those of rats from Catanduanes (Heaney et al., 1991) but are much smaller than those of the northern giant cloud rat, *Phloeomys pallidus* (Taylor, 1934, p. 395). Specimens from Mount Isarog and Catanduanes all have the dark brown pelage typical of this species (Fig. 23). The standard karyotype of *P. cumingi* (2n = 44, FN = 66) is quite distinct from that of *P. pallidus* (2n = 40, FN = 60), providing strong evidence that the two taxa are separate species (Rickart & Musser, 1993).

Specimens Examined—Total 13. Site 1 (3 PNM, 8 USNM); Site 10 (2 FMNH).

Rattus everetti (Gunther, 1879)

The common Philippine forest rat (Fig. 24) is a large (253.2 ± 43.9 g) rodent that occurs throughout the Greater Luzon, Greater Mindanao, and Mindoro Faunal Regions, as well as Camiguin and Panay (Heaney et al., 1998; Musser & Heaney, 1992). It was the most commonly trapped mammal at all sites but was significantly more abundant in lowland dipterocarp forest at 450 m and 900 m than in other habitats (Fig. 12; Table 1 of Rickart et al., 1991). Trap success in 1988 varied from 0.66% to 2.81% with coconut bait and from 0.29% to 1.0% with earthworms; trap success was significantly greater with coconut bait (χ^2 = 12.534; $P < 0.001$). Stomach contents of six snap-trapped specimens included seeds, green plant matter, and insect fragments. Captive animals readily accepted several types of fruit, acorns, peanuts, coconut bait, sweet potato, ant and beetle larvae, adult insects (cicada, cricket, cockroach, robber fly, longhorn beetle, weevil), and fresh flesh of *Apomys*, *Crocidura*, and a *Sphenomorphus* lizard. Earthworms and millipedes were marginally accepted; captives rejected some seeds and fruits, an orchid bulb, a caterpillar, large ants, rove beetles, a harvestman, tender young leaves, moss, a mushroom, and flesh of a conspecific. *Rattus everetti* is best described as a broad omnivore.

These rats were almost exclusively nocturnal. During the relatively dry conditions of the 1988 field study, only 3 (2.4%) of a total of 125 animals were taken during daylight hours. During the much wetter conditions in 1993–1994, two individuals (18%) were trapped between midday and 16:00. Animals were trapped in a variety of situations, often on steep terrain or above the ground surface. Many were trapped beside fallen logs, but rarely did they seem to be in clearly visible runways. We believe they are scansorial, often foraging above the ground surface. In a logged-over area at ca. 500 m elevation at Site 9 in November 1989, an adult male was shot at night while it was sitting ca. 3 m aboveground on top of a mass of fruits in a *Ficus minahassae*, feeding on ripe figs. An adult female was hand-caught about 4 m up

TABLE 11. Mean (± SD) and range of selected cranial and external measurements of adult murid rodents (Muridae) from Mt. Isarog, southern Luzon, Philippines. Sample size smaller than N is indicated by the number enclosed in parentheses after the range. Measurements taken from sample sizes of 2 and 3 are given as averages and their ranges. All measurements except weight are in millimeters.

Species	Sex	N	Basioccipital length	Interorbital width	Zygomatic breadth	Mastoid breadth	Nasal length
Phloeomys cumingi	M	2	—	—	—	—	—
	F	2	78.9	15.8	43.6	25.6	28.4
			77.6–80.2	15.1–16.5	43.4–43.8	25.5–25.7	28.0–28.7
R. everetti	M	12	49.6 ± 2.26	7.3 ± 0.24	24.8 ± 1.05	19.3 ± 0.57	20.0 ± 1.13
			44.9–52.2	7.1–7.6	22.9–26.5	18.2–19.8	17.8–20.9
	F	15	48.8 ± 1.95	7.2 ± 0.43	24.8 ± 1.20	19.0 ± 0.82	19.7 ± 0.82
			45.0–52.2 (13)	6.4–7.9	23.1–26.5 (11)	18.4–20.5	18.4–20.5
R. exulans	M	1	30.7	5.0	—	—	12.2
R. tanezumi	M	4	41.0 ± 2.66	6.2 ± 0.31	21.0	16.6 ± 0.82	15.1 ± 0.66
			38.8–44.8	5.7–6.4	20.3–21.7 (3)	15.6–17.5	14.7–16.1
	F	2	42.3	6.2	23.0	17.2	15.7
			39.8–44.8	6.0–6.5	21.9–24.0	16.9–17.5	15.3–16.1
Rhynchomys isarogensis	M	7	41.4 ± 0.30	6.8 ± 0.16	16.8 ± 0.46	15.3 ± 0.46	17.2 ± 0.50
			41.0–41.7	6.5–7.0	16.2–17.4	14.9–15.7	16.7–18.2
	F	6	40.8 ± 1.15	6.6 ± 0.26	16.7 ± 0.56	15.2 ± 0.43	17.0 ± 0.61
			39.3–42.4	6.4–7.1	16.0–17.6	14.7–15.8	16.3–17.8

in a tree at 16:00 in mossy forest at Site 17 on 25 April 1992.

Scats of viverrids collected in 1993–1994 at 1150 and 1450 m contained bones and fur of *R. everetti* (Table 12). This species and *Apomys musculus,* both predominantly nocturnal, are the only two species in old-growth forest at these elevations known to be prey of viverrid carnivores on Mount Isarog; the predominantly diurnal species have not been found in the scats (Balete, 1995).

The 1993–1994 mark–recapture study at Site 18 (Balete, 1995; Balete & Heaney, 1997) showed that this species has an estimated mean distance moved between captures of 73 m (range 0–244 m), with males traveling significantly farther than females. *Rattus everetti* moved significantly longer distances than *Apomys musculus,* which had an MDM of 42 m. Home range size of five individuals (two males and three females) was estimated to be 0.41 ha (range 0.08–0.99 ha). During the same period, the density of this species was 1.2 individuals/ha, the lowest among the small mammals in mossy forest except *Chrotomys gonzalesi* (Table 10), but its biomass of 333.3 g/ha was the second highest of all, next to *B. granti.*

There was little evidence of female reproductive activity during our study. Nulliparous females (N = 28) weighed 95–245 g, averaging 166.5 g. No pregnancies were noted, and the majority of females had inactive reproductive tracts. A few females taken in early May, at the end of our 1988 study, had enlarged reproductive tracts and appeared to be entering reproductive condition. For 21 females with placental scars (246 g, range 190–340 g, N = 20), the number of placental scars (including several multiple sets) ranged from one to 13; we suspect typical litter size to be between three and six. On nearby Catanduanes Island, nulliparous females weighed 110–270 g, primigravid females weighed 245–285 g, and multiparous females with placental scars weighed 280–350 g; the latter appeared to retain several sets of scars, making it impossible to estimate litter size (Heaney et al., 1991). On Leyte, three females had four to six placental scars (Rickart et al., 1993).

In contrast to females, many males caught in March, April, and May were in reproductive condition. Fourteen adult males (299 ± 47.0 g, range 225–390 g) had scrotal testes ranging from 6 × 8 mm to 15 × 28 mm in size. Scrotal testes also were recorded in two young adults (185 and 200 g, testes: 3 × 17 mm and 7 × 15 mm) and four subadults (159 + 51.5 g, range 105–225 g, testes: 4 × 7 mm to 6 × 11 mm). Juveniles consisting of six males (133 ± 7.0 g) and three females (95–125 g) also were taken in both March and April. At Site 18, a juvenile female weighing 68 g was captured in December 1993 (Balete, 1995). On Catanduanes, males with scrotal testes weighed

TABLE 11. *Extended.*

Anterior nasal width	Rostral depth	Rostral length	Orbital length	Maxillary molarifrom tooth row	Palatal breadth at P4	Diastema length
—	—	—	—	—	—	—
8.2	18.6	33.8	24.9	18.2	16.5	22.5
9.0–9.5	18.6–18.7	33.3–34.2	24.8–25.0	17.4–18.9	16.1–16.9	22.3–22.7
5.8 ± 0.25	11.2 ± 0.49	19.8 ± 1.05	18.1 ± 0.62	9.2 ± 0.31	9.2 ± 0.37	14.4 ± 0.92
5.4–6.2	10.3–11.7	17.8–21.4	17.0–19.1	8.6–9.7	8.9–9.9	12.7–15.4
5.4 ± 0.48	10.7 ± 0.45	19.2 ± 1.01	17.7 ± 0.61	9.0 ± 0.41	9.3 ± 0.32	13.8 ± 0.80
4.7–6.1	10.0–11.7	17.8–21.3	16.8–18.6	8.2–10.1	8.9–9.8	12.3–15.0
3.3	6.9	11.5	11.5	5.3	6.0	8.5
4.3 ± 0.26	8.9 ± 0.59	15.2 ± 0.91	14.9 ± 0.83	7.4 ± 0.41	7.8 ± 0.24	11.4 ± 0.55
4.0–4.6	8.2–9.6	14.4–16.5	14.3–16.1	6.8–7.8	7.5–8.0	11.0–12.2
4.5	9.2	16.3	15.5	8.0	8.3	11.7
3.9–5.1	8.7–9.7	15.5–17.1	15.0–16.0	7.7–8.3	7.8–8.8	11.4–12.0
3.3 ± 0.05	4.9 ± 0.32	20.6 ± 0.38	9.9 ± 0.24	2.2 ± 0.05	6.4 ± 0.25	13.9 ± 0.27
3.2–3.3	4.4–5.2	20.2–21.3	9.7–10.3	2.1–2.2	6.0–6.7	13.4–14.2
3.2 ± 0.05	4.7 ± 0.20	20.5 ± 0.51	9.8 ± 0.20	2.2 ± 0.10	6.3 ± 0.18	13.8 ± 0.33
3.2–3.3	4.5–5.0	19.7–21.0	9.6–10.1	2.1–2.3	6.1–6.6	13.3–14.2

230–240 g, and three subadults with abdominal testes weighed 190–230 g (Heaney et al., 1991).

Measurements are given in Table 11. Variation in size is substantial between islands within the Philippines (Heaney & Rabor, 1982; Heaney et al., 1991; Rickart et al., 1993); detailed analysis of geographic variation should be fruitful. Specimens from Mount Isarog, Catanduanes, and the Mindanao Faunal Region have a karyotype of 2n = 42, FN = 64, which is quite similar to the karyotypes of many Asian species of *Rattus* (Rickart & Musser, 1993).

SPECIMENS EXAMINED—Total 140. Site 1 (27 USNM); Site 2 (1 PNM, 35 USNM); Site 3 (25 USNM); Site 4 (15 USNM); Site 5 (10 USNM); Site 6 (13 USNM); Site 8 (1 UPLB); Site 9 (1 UPLB); Site 12 (1 UPLB); Site 13 (1 UPLB); Site 17 (1 FMNH, 2 PNM); Site 18 (4 FMNH); Site 20 (1 FMNH); Site 22 (2 FMNH); Site 23 (2 FMNH); Site 24 (2 FMNH).

Rattus exulans (Peale, 1848)

The Polynesian rat is a widespread commensal species found throughout the Philippines in disturbed areas associated with human habitation (Heaney et al., 1991, 1998). Our only records for Mount Isarog consist of specimens collected at 725 and 800 m by Rabor in 1961; we trapped none, despite intensive sampling. The elevational range of this species on the mountain (Sites 21 and 22) paralleled that of *R. tanezumi* (see below). Although Rabor (1966) provided no description of the vegetation at these sites, these specimens probably were taken in disturbed habitats. Measurements are given in Table 11.

SPECIMENS EXAMINED—Total 2. Site 21 (1 FMNH); Site 22 (1 FMNH).

Rattus tanezumi Temminck, 1844

The Oriental house rat (Fig. 24) is a widespread Asian species (formerly included in *Rattus rattus*; Musser & Carleton, 1993) that occurs throughout the Philippines, usually as a commensal in disturbed habitats close to human habitation (Heaney et al., 1998; Lepiten, 1997). However, on Philippine islands where the native rodent faunas are depauperate, this and other usually commensal species can be found in old-growth forest (Heaney et al., 1991; Heideman et al., 1987; Rickart et al., 1993).

On Mount Isarog, Rabor's records from Curry, Pili Municipality (Sites 19–22), indicated that this species was generally restricted to disturbed forest habitats and agricultural areas close to human settlements below ca. 800 m elevation. We captured none in 1988, despite intensive sampling in the forest. However, in December 1989 we captured

TABLE 11. *Extended.*

Species	Total length	Tail length	Hind foot	Ear	Weight (g)
Phloemys cumingi	692	280	84	36	1985
	671–712	274–287	82–85	34–37	1920–2050
	708	293	79	35	1893
	680–752 (3)	280–314 (3)	74–85 (3)	34–37 (3)	1850–1980 (3)
R. everetti	432 ± 29.9	215 ± 15.2	45 ± 2.2	26 ± 1.5	256 ± 56.4
	384–481 (28)	187–244 (28)	40–48	23–29 (28)	180–390 (29)
	425 ± 25.4	214 ± 18.7	44 ± 2.1	26 ± 1.5	239 ± 40.4
	366–474 (35)	181–239 (35)	38–47	22–29 (35)	170–340
R. exulans	—	—	—	—	—
R. tanezumi	—	—	—	—	—
	—	—	—	—	—
Rhynchomys isarogensis	294 ± 8.3	121 ± 3.2	39 ± 0.6	22 ± 0.8	125 ± 11.4
	280–305 (15)	115–126 (16)	38–40 (16)	21–23 (16)	110–145 (16)
	286 ± 8.6	115 ± 3.6	38 ± 1.0	22 ± 0.5	127 ± 14.0
	270–298 (9)	108–118 (9)	37–40 (9)	21–23 (9)	110–156 (9)

six *R. tanezumi* within the compound of the PLDT telecommunications relay station at 1450 m elevation on the southern slope of Mount Isarog (Site 16). Our sample consisted of an adult female with small mammae (228 g) and five juveniles of unknown sex (31.3 ± 4.06 g). The presence of the species at this facility, constructed in the 1960s within the upper montane forest zone, is clearly a legacy of past disturbance and the continued presence of humans in the area. Whereas these rats were common around the PLDT building, they were not taken in surrounding forest, where we caught *Archboldomys luzonensis, Batomys granti, Chrotomys gonzalesi, Rattus everetti,* and *Rhynchomys isarogensis.* This finding suggests that the species is restricted to heavily disturbed areas and is unable to colonize old-growth forest on the mountain.

The name *Rattus tanezumi* is used for the 2n = 42 group of Asian commensal rats that are distinguishable from the *R. rattus* group with 2n = 38/40 (Musser & Carleton, 1993; Rickart & Musser, 1993)

SPECIMENS EXAMINED—Total 13. Site 8 (1 UPLB); Site 15 (6 UPLB); Site 19 (1 FMNH); Site 21 (1 FMNH); Site 22 (3 FMNH).

Rhynchomys isarogensis Musser and Freeman, 1981

The Isarog shrew-rat (Fig. 25) was described in 1981 on the basis of a single specimen collected by Rabor in 1961 (Musser & Freeman, 1981). In 1988, we found this medium-sized murid (122.5 ± 9.5 g) to be common in montane and mossy forest from 1125 to 1750 m and to be absent from lowland forest; it was significantly more common in mossy forest than in other habitats (Table 1 of Rickart et al., 1991). Trap success ranged from 0.73% to 4.41% with earthworm bait and 0.07% to 0.19% with coconut bait. Overall trap success was greater with earthworms than with coconut bait (χ^2 = 58.812, $P < 0.001$). In 1993–1994, the mean density of this species was estimated to be 2.6 individuals/ha, twice that of *R. everetti,* and its biomass of 328.4/ha was only slightly lower than that of *R. everetti* (Table 10). We recorded movements of a single male, which was captured thrice in the span of 3 days, having moved an average of 50 m (range 40–60 m). Too few recaptures were made to estimate home range size (Balete & Heaney, 1997).

The stomachs of six snap-trapped specimens contained earthworms, amphipods, insect larvae, (Coleoptera, Diptera), and adult insects (Diptera, Orthoptera). None contained recognizable plant material. Two captives avidly accepted earthworms and readily accepted beetle grubs and pupae, amphipods, isopods, small millipedes, and adult crickets. Hard-bodied insects, small snails, meat of various rodents, and all plant material were unequivocally rejected.

Captives were especially adept at handling

TABLE 12. Composition of viverrid scats collected at various elevations on Mt. Isarog from December 1993 to April 1994. Plant samples in the scats consisted mainly of fruits (*Elaeocarpus luzonicus*) or flowers and leaves (*Freycinetia* sp.). Invertebrates were represented by ovipositors and exoskeleton (orthopterans) or elytra and legs (coleopterans). Remains of *Phloeomys cumingi* and a frog consisted entirely of bones, while those of *Apomys musculus* and *Rattus everetti* were comprised of bones and fur.

Date	N	Elevation (m)	Plants	Invertebrates	Vertebrates
12 Dec 1993	1	1150	*E. luzonicus*		*R. everetti*
			Unidentified		
16 Dec 1993	1	1550	*Freycinetia*	Orthoptera	*A. musculus*
20 Dec 1993	1	1550	*Freycinetia*		
3 Feb 1993	2	1150	*E. luzonicus*		*P. cumingi*
				Coleoptera	small frog
17 Feb 1994	2	1600	*Freycinetia*	Orthoptera	*A. musculus*
12 Apr 1994	1	1450			*R. everetti*

earthworms. Small earthworms (<1 g) were quickly ingested whole (end-on) with minimal processing. Larger worms were held with the forepaws and eaten progressively from one end. The thin, sharp incisors were used to tear off portions of the prey, which were swallowed whole. Periodically the mouth grip was transferred to a point 2–3 cm from the damaged end, and the worm's gut contents were extracted through this opening by vigorous squeezing and pushing movements with the forefeet. One captive consumed a 6-g worm in approximately 1 min. Our data indicate that *R. isarogensis* is a specialized vermivore but that other soft-bodied invertebrates are also included in the diet.

This species was predominantly nocturnal; out of a total of 32 animals captured in 1988, only 3 (9.4%) were taken during daylight hours. Animals were trapped exclusively on the ground in a variety of situations, most often in areas of moderate to dense cover. Most specimens were trapped on broad (5–8 cm) trails that were kept free of dead

FIG. 24. Adult *Rattus everetti* (below) and *R. tanezumi* (above), showing the relative size and proportions of these species. February 1988, Catanduanes Island, L. R. Heaney.

FIG. 25. Adult *Rhynchomys isarogensis*. 22 March 1988, Site 3, L. R. Heaney.

leaves and other obstructions; these trails could often be seen running for dozens of meters, merging with other trails. The basic morphology (gracile body form, long and muscular hind limbs, long but narrow hind feet, slender forefeet with small claws) and our observations of captives indicate that this species is a highly active saltatorial rat. We noted that the dorsal skin from shoulders to rump contained a tough, moderately thick matrix of connective fibers, quite unlike that of any other mammal in the Philippines; it is reminiscent of the dermal shields of elephant shrews (Rathbun, 1978).

Two pregnant females (115 and 125 g) taken in late April each had a single embryo (CRL = 6 and 10 mm). Five postpartum females (125 ± 11.2 g) taken in both March and April had one to three placental scars (including some with differences in degree of pigmentation that we interpret as being from several pregnancies). An adult female (128 g) collected in February 1994 had a single embryo (CRL = 1 mm). Ten adult males (126 ± 9.8 g) in breeding condition had scrotal testes ranging in size from 8 × 14 mm to 12 × 20 mm and convoluted epididymides. Three juvenile males (49.5–59 g) were also caught during March and April.

The karyotype is 2n = 44, FN = 52/53, and there are karyological similarities to *Chrotomys* and *Apomys* (Rickart & Musser, 1993). Measurements are provided in Table 11.

SPECIMENS EXAMINED—Total 38. Site 3 (1 USNM); Site 4 (6 USNM); Site 5 (3 USNM); Site 6 (22 USNM); Site 17 (2 FMNH, 2 PNM); Site 18 (1 FMNH).

Order Carnivora

Family Viverridae—Civets

Paradoxurus hermaphroditus (Pallas, 1777)

The common palm civet is found throughout the Philippines and much of Southeast Asia, where it is common in both agricultural areas and forests. A male with scrotal testes measuring 17 × 13 mm was trapped in March 1988 at 1550 m elevation (Site 5). On the evening of 29 December 1989, a young adult male was shot by a

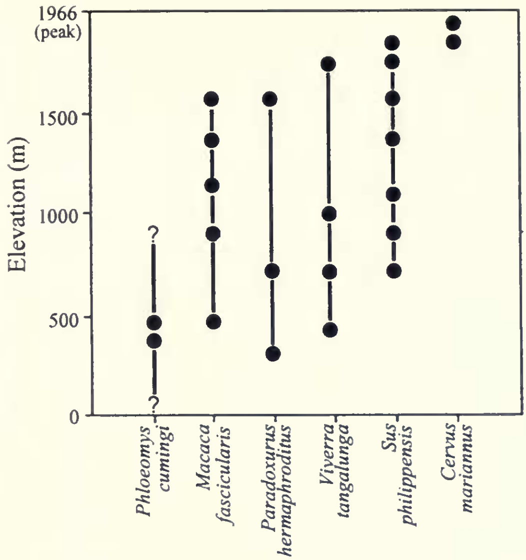

FIG. 26. Elevational distribution of large mammals on Mount Isarog.

local farmer as it was apparently feeding on ripe fruit high in a coffee tree growing in an agricultural area at 350 m elevation (Site 8). Another young male was shot at night by a hunter after being treed by dogs in disturbed forest at 700 m elevation (Site 12). A second male specimen from this site was caught in a native snare. Rabor's team took a specimen at 725 m, probably in disturbed lowland forest, in 1961. These records indicate that the species occurs over most or all of the elevational gradient (Fig. 26). We suspect that it is the more common of the two local viverrids.

The majority of scats collected in 1993–1994 at various sites between the lowland montane and mossy forest (Table 12) contained a combination of plant materials (mostly fruits of *Elaeocarpus luzonicus* and *Freycinetia* sp.) and remains of several rodents (bones and fur), including *Apomys musculus, Phloeomys cumingi,* and *Rattus everetti.* The omnivorous feeding habits of the predators that deposited these scats lead us to suspect that these were from *P. hermaphroditus.* This is consistent with the known feeding habits of this species (Alcala & Brown, 1967; Auffenberg, 1988; Bartels, 1964; Rabor, 1955, 1977).

SPECIMENS EXAMINED—Total 6. Site 5 (1 USNM); Site 8 (2 UPLB); Site 12 (2 UPLB); Site 18 (1 FMNH); unknown site (1 AMNH).

Viverra tangalunga Gray 1832

The Malay civet is found throughout much of Southeast Asia, including the Philippines, but is common only in forested habitats. We obtained two specimens from local hunters. The one from barangay Del Rosario was snared on 6 December 1989 in disturbed lowland forest at 700 m elevation (Site 12). The other was purchased on 24 March 1988 from a hunter who had snared it on the northeastern flank of the mountain at about 450 m in a patch of second-growth forest in an area that is dominated by agriculture. Rabor's crew took two specimens, one recorded as "3000–3500 ft" (Site 22) and another recorded as "5500 ft" (Site 23). Together, these records imply that Malay civets range from the bottom to the top of the mountain (Fig. 26).

Stomach contents of the specimen from barangay Del Rosario consisted mostly of slugs and land snails. Auffenberg (1988) suggested that *V. tangalunga* in Caramoan is largely carnivorous, feeding on rodents and freshwater crabs. An adult female from Leyte had stomach contents that included two large centipedes, one large snail, and at least one skink and one small snake (Rickart et al., 1993). Scats of viverrids collected in 1993–1994 (Table 12) contained mostly plant materials and remains of the rodents *Apomys musculus, Phloeomys cumingi,* and *Rattus everetti,* indicating they were eaten by an omnivorous predator, most likely palm civets (see account for *P. hermaphroditus*).

SPECIMENS EXAMINED—Total 1. Site 12 (1 UPLB); northeast flank of Mount Isarog (1 USNM); Site 22 (1 AMNH); Site 23 (1 AMNH).

Order Artiodactyla

Family Suidae—Pigs

Sus philippensis Nehring, 1886

The Philippine wild pig occurs within the Luzon, Mindanao, and Mindoro Faunal Regions, and was considered by Groves (1997) and Grubb (1993) to be specifically distinct from the other native pig species, *Sus barbatus* (occurring in the Palawan Faunal Region, Borneo, and the Malay Peninsula) and *S. cebifrons* (restricted to the Negros-Panay Faunal Region).

On Mount Isarog, local hunters told us that wild pigs were still present in the remaining old-growth and disturbed forest (Fig. 26), although they had become uncommon. In 1988, local people told us that it had been over a year since one had been caught; we saw several pit traps and one snare, and we were told that several settlers on the mountain were still engaged in pig hunting with the aid of hunting dogs. During 1989–1990, pig wallows and signs of foraging were commonly seen in disturbed forest at ca. 600–800 m elevation (Sites 12 and 13). On several occasions at Site 18, fresh tracks of wild pigs were encountered along creeks in the mossy forest. On 27 January 1990, a juvenile male was captured by a local hunter while it foraged near a dry creek at 700 m elevation (Site 12). The animal was less than 1 year old and probably recently weaned; most of the milk teeth were still present, but some of the permanent teeth were starting to erupt. This was said to be the first wild pig taken from the area in more than a year. Head plus body length = 620 mm; tail length = 60 mm.

SPECIMENS EXAMINED—Total 1. Site 12 (1 PNM).

Family Cervidae—Deer

Cervus mariannus Desmarest, 1822

This species is native to the Luzon, Mindanao, and Mindoro Faunal Regions of the Philippines and has been introduced to the Mariana, Caroline, and Bonin Islands (Grubb, 1993). This species and *C. alfredi* (restricted to the Negros-Panay Faunal Region) were formerly included within *C. unicolor* but were recognized as distinct species by Grubb and Groves (1983).

We received no recent reports of deer in low-elevation forest on Mount Isarog, and residents believed they had been gone from the lowlands for many years. However, at least some deer persist at higher elevations on the mountain. On several occasions in 1988 and 1990, we came upon fresh deer droppings and tracks in mossy forest between 1750 and 1850 m (Sites 6, 17, and 18; Fig. 26). Our guide in 1989–1990 said that nipped fiddleheads of low-lying tree ferns in the mossy forest had been browsed upon by deer.

Analysis and Discussion

Adequacy of Sampling

Surveys of the mammals of any region, especially in poorly known parts of the tropics, are rarely carried out with sufficient intensity or over sufficient periods of time that they can be considered complete or precise (Voss & Emmons, 1996). Accordingly, we must attempt to evaluate the degree of completeness of our data so that we may then make meaningful and appropriate comparisons to other sites. Our survey procedure consisted of (1) sampling extensively along elevational transects in all major types of habitat; (2) employing standardized sampling procedures; (3) plotting species–effort curves, which provide an index of the likelihood of captures of further species; and (4) estimating the relative abundance of individual species, to determine the habitat where they are most abundant (Heaney et al., 1989, 1991; Rickart et al., 1991, 1993). Whenever possible, we then supplemented the initial data with detailed studies, as Balete (1995) has done in this case.

We believe there are five principal habitats that need to be sampled to assess the mammal fauna on any given Philippine island: lowland forest, montane forest, mossy forest, second growth (at all elevations), and caves (Heaney et al., 1989, 1991; Rickart et al., 1993). In our surveys of Mount Isarog, we believe that the first three habitat types were adequately sampled. Very few natural caves occur on Mount Isarog itself, but there are caves in low-lying areas within 10 km of the mountain; our limited sampling of caves is a weakness of this study. The weakest portion of our survey is that of second-growth habitat, where we did only limited and incidental sampling. The accuracy and thoroughness of sampling also vary with taxonomic group and specific sampling techniques, so various groups need to be assessed differently. In the present study these include (1) large megachiropteran bats (*Pteropus* and *Acerodon*), (2) small megachiropterans (all other genera), (3) microchiropteran bats, (4) small rodents and insectivores, and (5) large, nonvolant species.

Our knowledge of the large megachiropterans of Mount Isarog is incomplete, largely because flying foxes typically fly well above the canopy and approach feeding trees from above, rarely descending low enough to encounter mist nets. At present, only two species are known with certainty (*Pteropus hypomelanus* and *P. vampyrus*, each

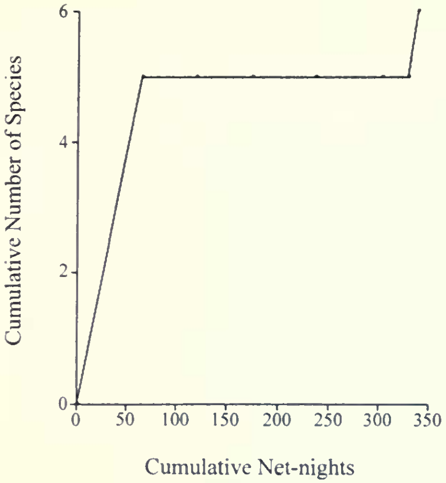

FIG. 27. Cumulative species–effort curve for the number of fruit bat species captured in nearly 350 net-nights in all habitats on Mount Isarog in 1988.

based on a single record), although we found indirect evidence for the occurrence of a third species (*P. leucopterus*). There is a strong possibility that two additional widespread species (Heaney et al., 1998) may occur on the mountain (*Acerodon jubatus* and *Pteropus pumilus*).

Recent studies of small megachiropterans in the Philippines indicate that our 1988 samples of 54–75 net-nights at Sites 1–5 (475–1550 m; Table 4) are likely to have yielded approximate species richness and proportional abundance, although rare species may have been missed (Heaney et al., 1989; Heideman & Heaney, 1989). On a replicate transect of more limited scope on the south side of the mountain in 1989–1990 (Sites 7–17) two additional species were found at very low elevations in agricultural habitat, thus extending the documented elevational range for several species (Fig. 13). A species–effort curve (Fig. 27) for the 1988 season shows a jump in species richness at the end of the season, when our persistent efforts yielded specimens of *Harpyionycteris whiteheadi*. At least one species that is now rare throughout the Philippines could occur in the area (*Eonycteris robusta*; Heaney et al., 1998), but capture of additional species at middle to high elevation on the mountain is unlikely because all other species known to occur in this part of the Philippines were netted. We conclude that our samples are likely to accurately reflect the number of species, relative abundance, and patterns of habitat use of small fruit bats on Mount Isarog, with the exception of one rare species (i.e., *Eonycteris robusta*).

Microchiropteran bats, which differ from megachiropterans in possessing the ability to echolocate, are difficult to capture in mist nets, and mist net studies typically result in underestimation of their diversity and abundance (Francis, 1989). Our sampling of microchiropterans in forests relied solely on mist nets, so we consider our data to be useful as indicators of general patterns but not suitable for detailed interpretation or comparison. More sampling using different techniques (especially harp traps) in forest, caves, and second-growth habitat would very likely increase the number of microchiropteran species.

Our trapping surveys of small rodents and insectivores were extensive. Previous studies have shown that in the Philippines, samples based on 900 or more trap-nights are effective in assessing species richness and approximately proportional abundance, although rare species may still be missed (Heaney et al., 1989; Rickart et al., 1991). Our studies on Mount Isarog in 1988 (described in detail by Rickart et al., 1991) included more than 1,100 trap-nights in all native habitat types and included two types of bait (fried coconut and live earthworms) at all sites. Species–effort curves (see Rickart et al., 1991) indicate that it is quite unlikely that additional species of small mammals remain to be trapped on the mountain as a whole, although some individual sites might yield small increases in species richness with the addition of some locally rare species (e.g., Site 5 at 1550 m). A less intensive replicate transect on the south side of the mountain in 1989–1990 did not yield any additional species or extensions in documented elevational range. On the basis of these data, we conclude that our sampling of the small mammal fauna probably yielded an accurate assessment of the number of species present on the mountain and probably showed their relative abundance and elevational range fairly precisely; i.e., some small changes in elevational range, relative abundance, and habitat associations may be documented by future studies, but we expect no major changes.

At present, there are six species of medium- or large-sized mammals known from Mount Isarog. These include one primate, one rodent, two carnivores, and two ungulates. We have no reason to suspect that there are any other large species on the mountain because their presence is generally easy to document (either directly or through local informants). We know that all but one species (*Phloeomys cumingi*) once utilized the entire elevational gradient and that all were once moder-

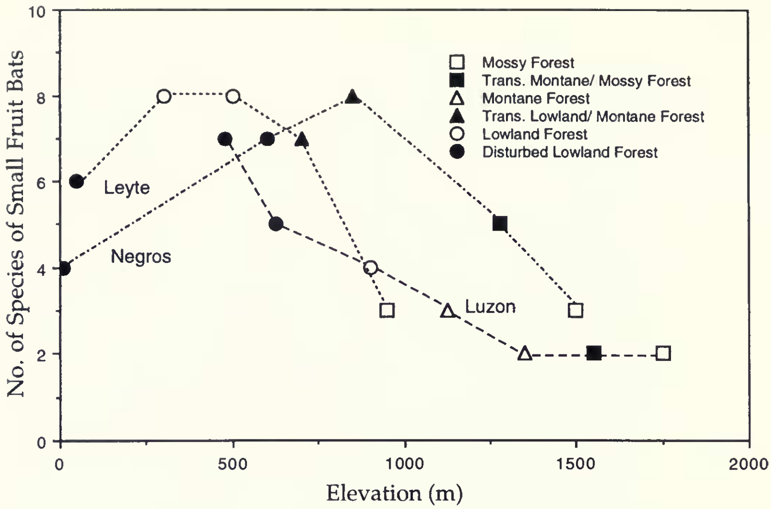

FIG. 28. Number of species of small fruit bats recorded along the elevational gradients on Mount Isarog (this study; Fig. 13), Mount Pangasugan, Leyte, and Mount Guinsayawan, Negros (Heaney et al., 1989).

ately common. However, we know few details about their use of the various habitats.

In summary, we believe our data on small nonvolant mammals to be strongest (with only minor changes in elevational range and abundance likely with more intensive study), that on small fruit bats to be sufficient for documenting patterns of species richness and abundance (but with documentation of rare species and some minor changes in elevational range possible), that on large mammals to indicate the species that are present (but little about patterns of abundance), that on insectivorous bats to indicate rough patterns of species richness (but with future studies likely to add substantially to the number of species), and that on large bats to be quite incomplete in all respects. On this basis, we now proceed to interpret the data in appropriate ways.

Patterns of Species Richness and Relative Abundance of Small Fruit Bats

Small fruit bats were most diverse at our lowest sampling sites on Mount Isarog, but species richness declined steadily with increasing elevation (Figs. 13 and 28; Fig. 28 is modified from Heaney & Rickart, 1990, on the basis of the 1989–1995 data in Fig. 13). The degree of similarity to the pattern on Leyte and Negros, the only two sites from which comparable data currently are available (Heaney et al., 1989; Heaney & Rickart, 1990), depends on the basis of comparison. On Mount Pangasugan, Leyte, the high species richness seen in the lowlands drops off quickly with increasing elevation, but the elevational gradient is truncated (the mountain peak stands at only 1150 m). On Mount Isarog and Mount Guinsayawan, Negros, which are similar in peak elevation at 1966 and 1788 m, respectively, the elevational decline in the number of species is much more gradual. However, when one compares the decline with respect to habitat type, the patterns become more similar (Fig. 28). On all three mountains, disturbed lowland forest has six or seven species and mossy forest has two or three species, with gradually declining numbers between. We conclude that the patterns follow vegetation and climatic changes that are associated with elevation and that elevation per se is less strongly correlated with species richness.

Netting success, which is our measure of abundance, also shows generally similar patterns on all three mountains (Fig. 29). We lack data on Mount Isarog from lowland agricultural areas that provided the highest densities of fruit bats on Leyte and Negros, but otherwise the pattern of decline is similar on all three mountains. The most conspicuous difference among them is the two- to threefold higher density on Negros than on the other islands; we have no ready explanation for this difference. An agricultural site on Catanduanes Island, which is quite close to Mount Isarog (Fig. 1; Heaney et al., 1991), had bat density and species richness comparable to that in mixed ag-

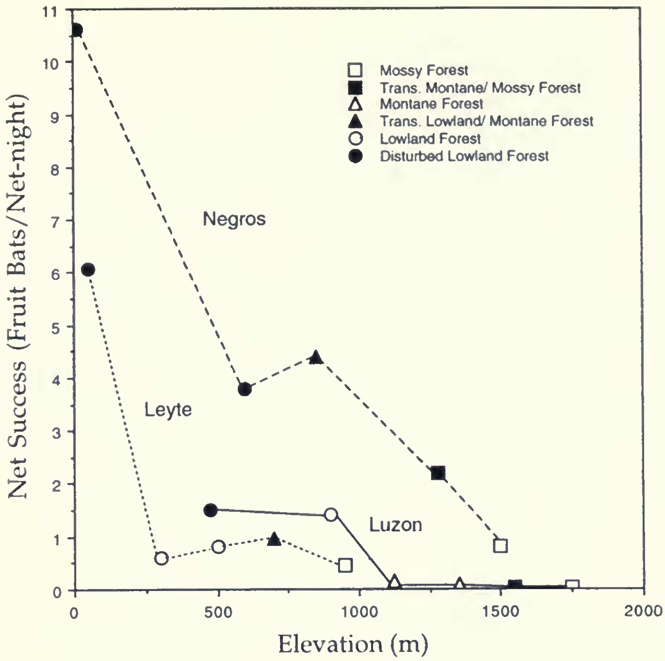

FIG. 29. Relative abundance of small fruit bats recorded along the elevational gradients on Mount Isarog (this study; Table 4), Mount Pangasugan, Leyte, and Mount Guinsayawan, Negros (Heaney et al., 1989).

ricultural land and secondary forest on Mount Isarog, but a single lowland forest site on Catanduanes had density and species richness lower than on Mount Isarog. When these data are again compared on the basis of habitat type rather than elevation, the consistency of the pattern increases. We conclude that the pattern of declining abundance of small fruit bats with elevation is consistent and probably primarily associated with changes in habitat rather than elevation per se, as was also the case for species richness.

Patterns of Species Richness and Relative Abundance of Nonvolant Small Mammals

Along our 1988 transect on the western side of Mount Isarog (Sites 1–6), the number of nonvolant small mammals was lowest in lowland forest (three species) and highest in montane and mossy forest (eight and seven species, respectively; Fig. 12, and Table 1 of Rickart et al., 1991). The number of species captured showed a general increase from lowland forest to montane and mossy forest, although different rank correlation measures yield different results: species richness was not significantly correlated with elevation (r_s = 0.80, $P >$ 0.05), but a strong positive trend was indicated by a significant association between ranked elevation and ranked species richness ($P < 0.05$, Olmstead Tukey test; Rickart et al., 1991). These results support an earlier prediction of increasing species richness with elevation by Heaney et al. (1989) and are in clear contrast with widespread patterns seen for bats and birds, among which maximum species richness is in lowland forest (Diamond, 1972; Graham, 1990; Heaney et al., 1989; Terborgh, 1977).

The relative abundance of nonvolant mammals, as measured by trap success, also varied with elevation (Fig. 30). The values represented for Mount Isarog are from the 1988 field season using the standardized sampling described in detail by Rickart et al. (1991), based on overall unweighted trap success (Table 2 in Rickart et al., 1991). The number of individuals captured showed a general increase from lowland forest to montane and mossy forest; although abundance was not significantly correlated with elevation (r_s = 0.80, $P >$ 0.05), deletion of the anomalous 1550-m site resulted in a significant correlation for unweighted overall success with the remaining sites (Rickart et al., 1991), which suggests a general increase in relative abundance with elevation, as predicted

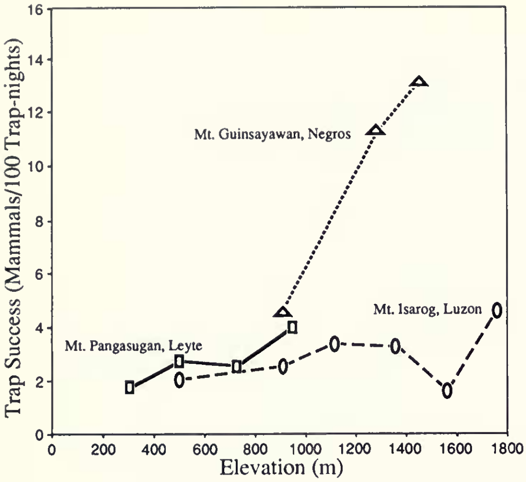

FIG. 30. Relative abundance of small mammals (insectivores and murid rodents) recorded along the elevational gradients on Mount Isarog (this study; Rickart et al., 1991), Mount Pangasugan, Leyte, and Mount Guinsayawan, Negros (Heaney et al., 1989).

from earlier studies on Leyte and Negros (Heaney et al., 1989). The exceptionally high relative abundance values from Negros are of interest because this community is composed of only two native species plus three non-native species, and the non-native species are much more abundant than the native species. Further studies of species richness and relative density on other mountains in the Philippines are needed to determine general patterns. The densities (measured as number per hectare, rather than as number per 100 trap-nights) recorded at Site 18 are among the highest known for small mammals in the tropics (Balete & Heaney, 1997).

Patterns of Species Richness of Microchiropteran Bats

No detailed estimates of Philippine microchiropteran faunal richness are available, and few comparisons are possible. With 14 species documented on the mountain and two others recorded nearby, Mount Isarog compares favorably with the 15 species recorded from Catanduanes (Heaney et al., 1991), 17 recorded from Leyte (Rickart et al., 1993), and 14 recorded within a single sampling area at 200–500 m on Mount Makiling, Laguna Province (Ingle, 1992).

We captured 82 microchiropterans on the mountain in 1988 at Sites 1–6; they represented 12 species (Table 7). Despite a similar netting effort at all but the highest elevation, we found a steady decline in species richness along the transect from seven to one species (Fig. 16), in a manner similar to that seen in small fruit bats (Figs. 13 and 28). No clear pattern was evident on Leyte, the only site with comparable transect data (Rickart et al., 1993). As noted above, these data should be taken only as rough indications of patterns, because our sampling of insectivorous bats was almost certainly incomplete.

There are few caves, rock shelters, or tunnels on or near Mount Isarog, and we captured only two species of insectivorous bats in such places (*Emballonura alecto* and *Miniopterus schreibersi*). The records of *Hipposideros bicolor* and *H. pygmaeus* from Pasacao may have originated from a cave, because these bats often roost in such places (Heaney et al., 1998).

Biogeography

Mount Isarog and the adjacent island of Catanduanes (Heaney et al., 1991) currently are the only sites in southern Greater Luzon where the mammalian faunas have been well studied (Heaney, 1986); only scattered records exist from the rest of the Bicol Peninsula and associated islands. Our comments on biogeography therefore must necessarily be based on very limited information.

The 44 native species of mammals known to occur on or near Mount Isarog constitute a large fraction of the 83 native species known from Luzon (Heaney et al., 1998). Current evidence suggests that the Bicol Peninsula constitutes a distinctive subregion of the Greater Luzon region. *Archboldomys luzonensis, Chrotomys gonzalesi,* and *Rhynchomys isarogensis* are currently known only from Mount Isarog. *Phloeomys cumingi* is known only from the Bicol Peninsula, the islands of Catanduanes and Marinduque, both of which were part of Greater Luzon during Pleistocene periods of low sea level, and the adjacent portions of central Luzon (Heaney, 1986; Oliver et al., 1993a). All four of these species have their sister taxa in central and northern Luzon (Rickart et al., 1991). As the highest forested peak in southern Luzon, Mount Isarog is likely to support the richest mammalian fauna in the region; current evidence is consistent in showing that the maximum diversity of nonvolant mammals in the Philippines (which are especially rich in endemic species) is associated with areas of high topographic diversity that retain old-growth forest cover (Heaney et al., 1989; Rickart et al., 1991; Heaney, unpubl. data). However, this hypothesis is in need of careful testing, which can be accomplished only by intensive survey of other mountains on the Bicol Peninsula.

Four mountain peaks on the Bicol Peninsula hold potential for testing the impact of topographic diversity on mammalian diversity: Mount Iriga, Mount Malinao, Mount Mayon, and Mount Bulusan (Fig. 1). In a recent brief survey of Mount Bulusan at the southernmost tip of Luzon, D. S. Balete found only scattered remnant forest on the mountain, with volcanic eruptions, extensive logging, agricultural clearing, and storm damage having contributed to the destruction of the natural vegetation. A limited amount of trapping yielded only *Rattus everetti* and *R. tanezumi,* and netting yielded only common fruit bats, which are highly tolerant of disturbance (specimens in FMNH and PNM). It is unlikely that any habitat remains on Mount Bulusan that could support the endemic mammals of the Bicol Peninsula, with the exception of *Phloeomys cumingi,* which is relatively tolerant of disturbance (see species account).

Mount Mayon, the tallest mountain on the Bicol Peninsula at 2421 m, is an active volcano that erupts frequently. The upper portion of the mountain is covered by exposed volcanic ash flows, welded ash, and lahars; the lower portions are covered by a mixture of ash flows, disturbed forest, and agricultural fields. It seems an unlikely place to support populations of the endemic mammals.

Mount Iriga, which reaches 1337 m, is now almost completely denuded of natural vegetation up to the peak, and we doubt that it supports any endemic species at present.

Mount Malinao, which reaches 1548 m, is a dormant volcano midway between Mount Mayon and Mount Iriga (Fig. 1). The lowland forest is extensively fragmented, with virtually all lowland areas heavily cultivated and populated by humans, but portions of the montane and mossy forest remain intact. Of the four poorly studied high peaks on the Bicol Peninsula, this is the one most likely to support populations of the species currently known only from Mount Isarog. To the best of our knowledge, no surveys of the mammals of Mount Malinao have been conducted.

Another interesting and important point of comparison is Mount Banahaw, the highest peak (2165 m) between Mount Isarog and the two mountain ranges of northern Luzon, the Central Cordillera and the Sierra Madre (Fig. 1). This mountain might represent either the northernmost point of the Bicol fauna, the southernmost point of the northern mountain fauna, a mixture of the two, or, depending on its degree of isolation, another local center of endemism. In an unpublished M.Sc. thesis, Rosell (1996) reported the presence of an unidentified *Rhynchomys,* as well as four species of *Apomys,* reinforcing the importance of study and publication on this exciting site.

Distribution and Ecology of Non-native Species: Are They a Threat to Native Murids?

A subject of increasing interest to conservation biologists and managers is the impact of non-native (= exotic) species on the native organisms in protected areas. On oceanic islands, introduced species often have been able to invade old-growth habitats and displace the native species (e.g., Atkinson, 1989; Case, 1996; Ebenhard, 1988). Goodman (1995) recently suggested that *Rattus rattus,* a non-native species on Madagascar, is displacing endemic murids in forests on Madagascar and suggested that other communities of endemic murids might be similarly affected in many protected areas in the tropics, especially on islands.

Our data from Mount Isarog, although not designed specifically to investigate this issue, are highly relevant. We sampled extensively in both disturbed and old-growth lowland forest adjacent to agricultural land where commensal rats are abundant, including *Rattus tanezumi,* which is closely related to *Rattus rattus.* The results showed that the non-native murids that occur in the vicinity are entirely absent from forest on Mount Isarog; we captured only a few of the non-native species, and those only in or immediately adjacent to occupied buildings. In second-growth lowland forest that was regenerating under a scattered canopy of a non-native legume (*Leucena leucocephala*), we captured the native *Crocidura grayi, Apomys microdon,* and *Rattus everetti* and no *Suncus murinus, Mus musculus, Rattus exulans,* or *Rattus tanezumi,* which are common in and around human dwellings and in agricultural areas. This was the case even where a radio relay station (where non-native rats were present during our study) had been in place for more than three decades. We conclude that on Mount Isarog, commensal species of mammals are unable to displace the native species in either old-growth natural habitat (i.e., old-growth lowland forest) or disturbed but regenerating natural habitat adjacent to agricultural areas where non-native species are common. We found similar results on Leyte Island, where *Rattus tanezumi* was limited to heavily disturbed second growth adjacent to agricultural fields and was absent from all areas of old-growth forest (Heaney et al., 1989; Rickart et al., 1991).

However, we found quite different conditions on Negros Island (Heaney et al., 1989; Heideman et al., 1987). Negros has a depauperate native small-mammal community, consisting solely of a shrew (*Crocidura negrina*) and a forest mouse (*Apomys* sp.). In all forest habitats at all elevations on Negros, whether disturbed or old growth, we found that the commensal species *Suncus murinus, Rattus exulans,* and *Rattus tanezumi* dominated, with the native species present in smaller numbers. Similarly, we found *Suncus murinus* and *Rattus exulans* (but not *Rattus tanezumi*) to be common in forest on Camiguin Island, where there are only five native species of small mammals (Heaney & Tabaranza, 1995).

These observations led us to propose the hypothesis that the number of species in the native community of small mammals determines the success of non-native small mammals in invading native habitat on oceanic islands. Where few native species are present (e.g., Camiguin and Negros), the non-native species flood into the forest; where many native species are present, few or no non-native species are able to invade undisturbed habitats. This hypothesis could easily be tested on other islands in the Philippines, where there is great variation in the richness of the small-mammal fauna (Heaney, 1986). It could also be tested in forest fragments on the larger islands; for example, we predict that a patch of restored natural forest isolated from undisturbed native vegetation and thus with no source of colonizing native species could easily be invaded by non-native species, whereas a regenerating natural forest at the edge of native forest (which has a source of native small mammals) would be highly resistant to invasion by non-native species. Testing this hypothesis could produce information of great value to conservation and biodiversity managers.

Conservation and Management of the Mount Isarog Mammalian Fauna

The 48 species of mammals currently known from or near Mount Isarog include species that vary greatly in their breadth of distribution, range of abundance, and conservation status. Four species (*Suncus murinus, Mus musculus, Rattus exulans,* and *Rattus tanezumi*) are not native and will not be discussed further in this section. The others fall into six broad categories.

The first category is composed of three species that we believe once occurred on Mount Isarog but appear to no longer be present: *Hipposideros bicolor, H. pygmaeus,* and *Bullimus luzonicus.* As noted in the species accounts, there are no verified records of these species on the mountain, but all have been found nearby. Although there are no nearby records, we suspect that *Eonycteris robusta,* a widespread endemic fruit bat (Heaney et al., 1998), also once occurred on Mount Isarog. The three bats are all associated with caves in lowland forest (Heaney et al., 1998). Aside from the small tunnels at several sites that are near small patches of second-growth forest, there may be no caves left anywhere near Mount Isarog that have not been heavily disturbed by guano miners and bat hunters, and probably few to none that have forest nearby because of virtually complete clearing of the lowlands. *Bullimus luzonicus* is proving to be rather enigmatic; although it was recorded frequently up through about 1965, we know of few recent records, and those seem to be associated with bamboo. We regard these species as being of special concern, especially in southern Luzon, but also throughout the country; additional surveys are needed to determine their status and habitat needs and to develop recommendations for protection programs that will ensure their continued existence.

The second category consists of three species of bats that we detected in our samples but were uncommon: *Eonycteris spelaea, Rousettus amplexicaudatus,* and *Miniopterus schreibersi.* All are usually common in the Philippines, but we found only a few. All of these bats require caves as roosting sites; their relative rarity suggests that caves in the area of Mount Isarog have been severely disturbed by human activity and can no longer support large populations of these bats. We regard these data as reinforcing the conclusion that protection for caves should be made a high priority in southern Luzon.

The third category consists of seven species that are less common than formerly because of the combination of habitat destruction and overhunting. These species include the large fruit bats (*Pteropus hypomelanus, P. leucopterus,* and *P. vampyrus*) that once were common in forested habitats but are now quite uncommon in most places in the Philippines (Heaney et al., 1998; Mickleburgh et al., 1992; Utzurrum, 1992) because of both overhunting and destruction of lowland forests. Also included in this category are the long-tailed macaque (*Macaca fascicularis*), *bugkun* (*Phloeomys cumingi*), Philippine wild pig (*Sus philippensis*), and Philippine brown deer (*Cervus mariannus*), all of which have been and continue to be hunted so heavily on the mountain that their populations (especially the deer) are severely depleted and local extinction of most of these large mammals seems likely in the near future (Oliver et al., 1992, 1993a,b). Hunting in the park should be stopped immediately so that the populations may recover. If protection is provided, recovery of the populations seems likely, at which point sustainable hunting along the border of the park might be assured for the future. There was no protection against hunting during our study periods.

The fourth category consists of species that appear to survive only in lowland old-growth or good secondary forest, both of which continued to be depleted in most areas on the mountain during our studies. Such animals as *Haplonycteris fischeri, Harpyionycteris whiteheadi, Hipposideros obscurus, Megaderma spasma, Harpiocephalus harpia,* and *Philetor brachypterus* are widespread in the Philippines but are known on Mount Isarog only from lowland forest, which has been reduced to a narrow band of vegetation at the upper edge of its elevational range. These species are suffering similar habitat reductions elsewhere in the country, making them increasingly vulnerable to the effects of declining population size (including loss of genetic variability, increasing vulnerability to disease and climatic perturbations, etc.). This situation points to the loss of lowland forest across the Philippines as the single most serious problem for the protection of biological diversity (Heaney & Regalado, 1998). Because even second-growth lowland forest on Mount Isarog provided habitat for these species, as well as for such species as *Crocidura grayi, Apomys microdon, Phloeomys cumingi, Viverra tangalunga, Sus philippensis,* and *Cervus mariannus,* we recommend that all second-growth lowland forest on Mount Isarog be protected. This lowland forest should be allowed to regenerate with native forest and should not be planted with exotic species of trees such as *Gmelina* and *Eucalyptus*.

The fifth category includes the species that are endemic to the mountain: *Archboldomys luzonensis, Chrotomys gonzalesi,* and *Rhynchomys isarogensis*. The presence of this many species confined to a single mountain is quite extraordinary; generally, only isolated oceanic islands in the Philippines such as Sibuyan and Camiguin have so many unique species because of their historical geological isolation from other land masses (Heaney, 1986; Heaney et al., 1997, 1998). Fortunately, all three endemic species occur at the higher elevations on the mountain where habitat disturbance has been minimal. However, the fact that they occur nowhere else in the world makes them entirely dependent on the continued existence of all remaining old-growth forest on the mountain and justifies the concerns about their status that have been expressed (e.g., Baillie & Groombridge, 1996; Heaney & Utzurrum, 1991; Heaney et al., 1997, 1998). This observation points clearly to the need for effective protection of all remaining natural habitat in the park to prevent these highly distinctive and appealing creatures from disappearing from the one place where they live.

The sixth category consists of the 21 species not listed above that are widespread and believed to have currently stable populations. Although their present status is reason for a sense of relief that not all of the native fauna is endangered, it is not reassuring that fewer than half of 44 species known from the mountain fall into this category. Furthermore, without adequate protection of remaining forest habitat, it is certain that many additional species will become threatened in the near future.

Further study may alter our estimation of the status of any of the species on Mount Isarog, but the broad results are unlikely to change. It is clear that the remaining forest on Mount Isarog is essential to the survival of a remarkable set of species found nowhere else, that the lowland forest (both old growth and second growth) that now remains in the park is home to a large number of species which are increasingly vulnerable, that overhunting is a severe problem which needs to be reduced immediately, or some of the most appealing species will soon disappear, and that caves in southern Luzon are a resource that has been badly abused, with special measures needed throughout the country to protect this unique ecosystem.

Conclusions

Although each place in the Philippines is unique, it seems that Mount Isarog is a microcosm that is representative of many of the patterns that we see in the Philippines as a whole. The mountain is volcanic in origin and has been strongly influenced by subduction of the Pacific Plate under an island arc that has been one of the most geologically active places on earth. The mammal fauna on the mountain is diverse and is rich in both regional and local endemics at a level that is rarely equaled elsewhere in the world. Changes in habitat along the elevational gradient are associated with profound climatic changes (most remarkable is the increase in rainfall by a factor of five), and a great deal of the mammalian diversity on the mountain is associated with this climatic and habitat diversity. Bats and the nonflying small mammals show opposite trends in diversity and abundance along this elevational gradient, as we have seen elsewhere in the Philippines.

Other, less pleasant patterns on Mount Isarog also are representative of the Philippines as a whole (Heaney and Regalado, 1998). The lowland dipterocarp rain forest has been all but entirely destroyed; Mount Isarog retains one of the few patches in southern Luzon, and that exists only as a thin band at the upper edge of its former elevational range. We heard chain saws virtually every day in the park, and the roar of the last of the lowland forest trees as they crashed to the ground. Species that formerly were widespread and abundant in the lowland forest are now either uncommon or absent from the park; those that lived in caves in the lowlands have been most severely affected. Species in the park that are large enough to be of interest to hunters have been severely overhunted and currently are given no protection. The human hand lies heavily on Mount Isarog.

Fortunately, there is some good news as well. Exotic commensal species of small mammals are not successfully invading the park and displacing the native species; where the forest remains, the native species are holding their own. Only three species are believed to be locally extinct; the others that are locally (or nationally) endangered could probably recover if given an opportunity. Best of all, current community development programs at the border of the park, led by the Haribon Foundation, offer the hope of a more stable and perhaps sustainable style of life for the local people (Heaney & Regalado, 1998). In 1996, it was evident that some grasslands were gradually being reforested and that poaching had declined. Moreover, the improving national economy may help to draw people into activities that place less pressure on the land.

From the fertile plains of southern Luzon, Mount Isarog rises as a giant green mass, home to most of what remains of the natural heritage of the people of Bicol. Let us hope that it remains green, as a source of clean, clear water, as a site for recreation and learning about nature, and as the last refuge of the native flora and fauna that, like the people, call this their home.

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